

**Input data and parameter estimates
for ecosystem models
of the northern Gulf of St. Lawrence (2003-2005)**

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ABSTRACT

Savenkoff, C., S. Valois, D. Chabot, and M. O. Hammill. 2009. Input data and parameter estimates for ecosystem models of the northern Gulf of St. Lawrence (2003–2005). Can. Tech. Rep. Fish. Aquat. Sci. 2829: vi+117 pp.

Mass-balance models were used to reconstruct trophic flows through the whole northern Gulf of St. Lawrence ecosystem (NAFO divisions 4RS) for the 2003–2005 period. The whole-system model of the northern Gulf of St. Lawrence is divided into 31 functional groups or compartments from phytoplankton and detritus to marine mammals and seabirds, including harvested species of pelagic, demersal, and benthic domains. We present here details of the input data (biomass, production, consumption, export, and diet composition) for each compartment used for modelling. The parameter estimates from inverse modelling are also shown for comparison.

RÉSUMÉ

Savenkoff, C., S. Valois, D. Chabot, and M. O. Hammill. 2009. Input data and parameter estimates for ecosystem models of the northern Gulf of St. Lawrence (2003–2005). Can. Tech. Rep. Fish. Aquat. Sci. 2829: vi+117 pp.

Des modèles d'équilibre de masse ont été utilisés pour représenter les flux trophiques de l'écosystème complet du nord du Golfe du Saint-Laurent (divisions 4RS de l'OPANO) pour la période 2003–2005. L'écosystème du nord du Golfe du Saint-Laurent a été divisé en 31 groupes ou compartiments trophiques depuis le phytoplancton et les détritiques jusqu'aux oiseaux et mammifères marins incluant les espèces commerciales des domaines pélagique, démersal et benthique. Nous présentons ici le détail des données (biomasse, production, consommation, export et composition alimentaire) pour chaque groupe utilisé pour la modélisation. Les paramètres estimés par la modélisation inverse sont également montrés pour comparaisons.

INTRODUCTION

Mass-balance models have been constructed using inverse methodology for the northern Gulf of St. Lawrence for the mid-1980s, the mid-1990s, and the early 2000s to describe ecosystem structure, trophic group interactions, and the effects of fishing and predation on the ecosystem for each time period (Savenkoff et al. 2007). The two first models were carried out under a multidisciplinary and inter-regional program known as CDEENA (Comparative Dynamics of Exploited Ecosystems in the Northwest Atlantic), a program supported by the Canadian Department of Fisheries and Oceans (Science Strategic Fund).

This report presents the data and input parameters used to construct a new inverse model of the northern Gulf of St. Lawrence ecosystem (NAFO divisions 4RS) during the 2003–2005 period. Throughout the modelling process, different approaches (comparisons of different flow networks, random perturbations, sensitivity tests, etc.) were applied to assess the solution's robustness to variations in the data as well as to provide an overall view of the ecosystem, to identify robust patterns, and to determine the location of uncertainties in the food web. The estimated values from this final solution are presented here, along with the input parameters, to facilitate comparisons between inputs and outputs of inverse modelling.

MATERIAL AND METHODS

Model structure

Inverse methods are mathematical techniques used to generate a “snapshot” of the system at one time. They use mass-balance principles and an objective least-square criterion to estimate flows of organic matter or energy among trophic groups of an ecosystem (Savenkoff et al. 2004a). These models consider the ecosystem as a whole rather than its components separately and thus provide a description of trophic interactions between all functional groups of the ecosystem. The inverse approach solves flow networks by finding the solution that minimizes (objective least-square criterion) both the sum of squared flows (and thus the total sum of energy flows through the food web) and the sum of squared residual errors (i.e., minimizes the imbalances between inputs and outputs) consistent with the constraints (Vézina and Platt 1988). Inverse methods provide a powerful tool to estimate ecosystem flows using limited data and straightforward mass balance and metabolic constraints.

In the inverse approach, we use local measurements (e.g., catches), information on the trophic structure of the ecosystem (e.g., diet composition), and measurements of specific processes (e.g., production and consumption) to reconstruct the interactions and to estimate flows (in $\text{t km}^{-2} \text{ yr}^{-1}$; see Appendix 1) such as respiration, egestion, predation, or mortality due to factors other than fishing or predation for each functional group. Ecosystem inverse modelling is based on combining compartmental mass balance equations with data equations and eco-physiological constraints on the energy flows (Savenkoff et al. 2004a). The mass balance equations specify that, for each consumer group, the sum of inflows (consumption) is balanced by the sum of outflows (production, respiration, and egestion), a net change in the biomass variable (ΔB_i) and a residual term (ϵ) (Appendix 2). We assumed that there was no change in biomass ($\Delta B_i = 0$) during each time period and that net migration was zero (migration out of or into the study area, food intake

of predators that are not part of the system, etc.) (steady-state assumption). Also, production was equal to the biomass lost to fishing, predation, and natural mortality other than predation (hereafter termed other mortality causes). Other mortality causes include other natural causes of death such as disease or could reflect unsuspected processes occurring in the ecosystem, such as misreported catch (e.g., Savenkoff et al. 2004a), unsuspected migration, or other processes not accounted for in the model.

For phytoplankton and detritus, the general mass-balance equation was simplified. For the phytoplankton group, the net (corrected for respiration) production must balance the sum of the outputs (phytoplankton mortality including the egestion term and consumption of phytoplankton). For the detritus group, the inputs (egestion and other natural causes of death for other groups) must balance the sum of the outputs (consumption of detritus, bacterial remineralization of detritus, and burial). As bacteria were considered part of the detritus, detritus is assumed to respire.

With the compartmental mass-balance equations, the general structure of an inverse model also includes data equations and constraints. The data equations attempt to fix the value of certain flows or combinations of flows (e.g., incorporate the observations into the model that coincide with the period/region for which a solution was tested) while the constraints incorporate general knowledge into the model. The input data introduced directly into the model as data equations generally included values for exports (catches) from the system, production, and diet proportions locally estimated from field studies (Appendix 2). Data equations are also used for diet proportions available only as point estimates (no variance estimate) or with low observed values (i.e., $< 0.5\%$) and low uncertainty (i.e., $SD < 0.6\%$).

Additional constraints were needed to incorporate general eco-physiological knowledge into the model (Appendix 3). Each flow was taken to be non-negative, and flows and ratios of flows (metabolic efficiencies) were assumed to fall within certain ranges to satisfy basic metabolic requirements (Appendix 3). Gross growth efficiency (GE) is the ratio of production to consumption and for most groups should have values between 10 and 30% (Christensen and Pauly 1992). Exceptions are top predators, e.g., marine mammals and seabirds, which can have lower GE (between 0.1 and 1%), and small, fast-growing fish larvae or nauplii or bacteria, which can have higher GE (between 25 and 50%) (Christensen and Pauly 1992). Following Winberg (1956), 80% of the consumption was assumed to be physiologically useful for carnivorous fish groups while the non-assimilated food (20%, consisting of urine and feces) was directed to the detritus. For herbivores, the proportion assimilated could be considerably higher, e.g., up to 40% in zooplankton (Christensen and Pauly 1992). We constrained the assimilation efficiency (AE) to fall between 70 and 90% for all groups except for large and small zooplankton (between 50 and 90%). Certain flows have minimum and maximum values imposed (production, consumption, other diet proportions with higher values [e.g., $> 0.5\%$], export for detritus, etc.) and were incorporated as constraints (Appendix 3). To facilitate comparisons with other ecosystem models, we added constraints on the ecotrophic efficiency (EE). The ecotrophic efficiency is the fraction of the production that is either passed up the food web or exported. These values should be between 0 and 0.95 (Christensen and Pauly 1992, 1998). Here, a value only slightly above zero indicates that the group is not consumed in noticeable amounts by any other group in the system (e.g., top predators). Conversely, a value near or equal to 0.95 indicates that the group is heavily preyed upon and/or highly exploited by a fishery, leaving no individuals

to die of other causes (e.g., small prey organisms). Note that (1-EE) represents the natural mortality other than predation or other mortality causes (MO).

The choice of weights for each mass balance equation (called row weights) and for each unknown flow (column weights) is an important part of the solution process. In this study, the variances of the observed data were used as the row weights and the variances of the unknown flows as the column weights. We used the inverse of the variances in the weighting scheme, which limited the influence of large uncertainties on the solution. The weighting scheme does two things: (1) it introduces a prior hypothesis about the relative sizes of the unknown flows, (2) it limits the influence of large uncertainties on the solution; e.g., the weighted optimal fits were largely determined by the parts of the ecosystem about which we know the most. For each seal group, the biomass was estimated from the model of Hammill and Stenson (2000). We did not use these very low variances (SD^2 ; CV between 2% and 7%) in the scaling (or weighting) of inverse modelling. We used the average of all observed coefficients of variation for biomass (51%) obtained for all trophic groups as scaling factors for respiration, egestion, and natural mortality other than predation of each seal group; i.e., the unknown flows not related to observed input data. For each predation flow, we used the weighting scheme defined by Savenkoff et al. (2004a) to reduce numerical instability and give less weight to predation equations compared to other mass-balance equations in the solution. Indeed, there was a large number (94 of 361) of proportion of prey u in diet (by mass) of consumer y values that were low ($< 0.1\%$) or equal to 0% (representing a trophic relation between prey and predator in other ecosystems or another time period). This gave less weight to predation equations, allowing greater differences between initial and final estimates of diet proportions and reducing numerical instability.

Mass-balance models are deterministic and require many input parameters, some of which may be poorly known or adapted from other ecosystems. To explore the effects of uncertainty on the model results, a perturbation analysis was carried out once the initial balanced solution was obtained. We randomly perturbed each term by up to its standard deviation in order to represent the true uncertainties of the input data. Assuming uniform distribution, each x_i term was thus replaced by $x_i + rn \cdot SD_i$, where rn is a randomly chosen real number between -1 and 1 and the inverse analysis was recalculated each time (Savenkoff et al. 2004a). The final solution is always the mean of one solution without perturbation (the "initial solution") and 30 iterations with random perturbations of the input data (to a maximum of their standard deviations). This number is a compromise between limitations in computing time (one week for 31 balanced and ecologically realistic random perturbations) and statistical significance. The estimated values from this final solution are presented in Appendix 4.

Study area

The study covers an area of the northern Gulf of St. Lawrence (NAFO divisions 4RS), equivalent to $103,812 \text{ km}^2$ (Fig. 1). The nearshore region (depths $< 37 \text{ m}$) was not included in the model. Infra-littoral species such as American lobster (*Homarus americanus*) were not included in this study. This zone was excluded from the model because it is not covered by annual summer bottom-trawl surveys and because exchanges between the infra-littoral and offshore zones are still poorly understood. Half the northern Gulf is characterized by deep channels ($\geq 200 \text{ m}$), particularly the Laurentian Channel. The official sampling area used in our models for the

calculation of densities represents the surface of strata sampled during the summer scientific survey in the northern Gulf of St. Lawrence. The period covered by this analysis was from 2003 to 2005. However, there was no scientific trawl survey in 2004.

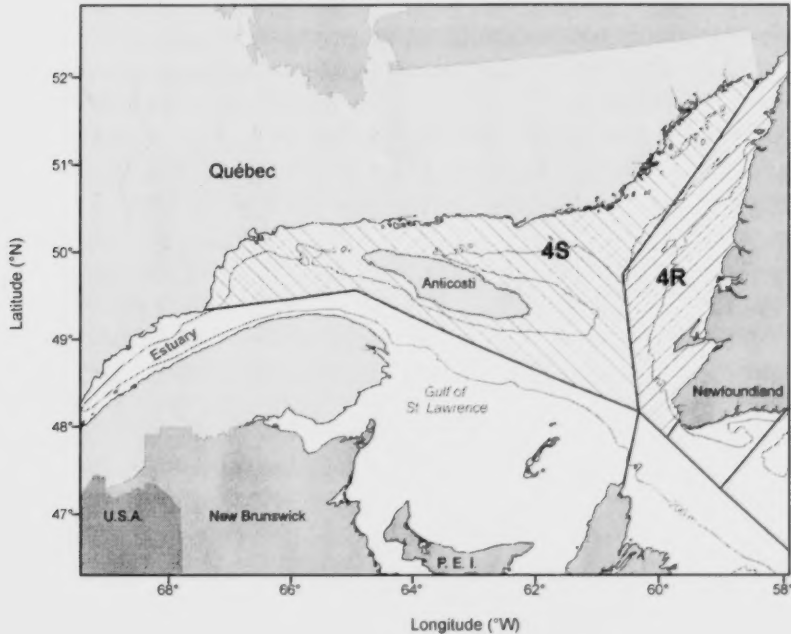


Figure 1. Northern Gulf of St. Lawrence (Northwest Atlantic Fisheries Organization [NAFO] divisions 4RS), equivalent to a total area of 103,812 km².

Functional groups

Based on data availability and the ecological and commercial significance of the species, the trophic food web is depicted by a number of compartments or functional groups representing the main pelagic, demersal, and benthic species present, which are interconnected by mass flows of matter. The whole-system model of the northern Gulf of St. Lawrence was divided into 31 functional groups or compartments (Table 1). We distinguished five marine mammal groups, one seabird group, fourteen fish groups, nine invertebrate groups, one phytoplankton group, and one detritus group (Table 1).

Table 1. Functional groups used in modelling for the 2003–2005 period.

Group Name	Main species
Mysticeti or baleen whales	Fin whale <i>Balaenoptera physalus</i> , minke whale <i>Balaenoptera acutorostrata</i> , humpback whale <i>Megaptera novaeangliae</i>
Odontoceti or toothed whales	White sided dolphin <i>Lagenorhynchus acutus</i> , white beaked dolphin <i>L. albirostris</i> , common porpoise <i>Phocoena phocoena</i>
Harp seals	<i>Pagophilus groenlandica</i>
Hooded seals	<i>Cystophora cristata</i>
Grey seals	<i>Halichoerus grypus</i> , harbour seals ^a <i>Phoca vitulina</i>
Seabirds	Double-crested cormorant <i>Phalacrocorax auritus</i> , ring-billed gull <i>Larus delawarensis</i> , herring gull <i>L. argentatus</i> , great black-backed gull <i>L. marinus</i> , common tern <i>Sterna hirundo</i> , Arctic tern <i>S. paradisaea</i> , black guillemot <i>Cephus grylle</i> , northern gannet <i>Morus bassanus</i> , black-legged kittiwake <i>Rissa tridactyla</i> , common murre <i>Uria aalge</i> , razorbill <i>Alca torda</i> , Atlantic puffin <i>Fratercula arctica</i> , Leach's storm-petrel <i>Oceanodroma leucorhoa</i>
Large Atlantic cod (> 35 cm)	<i>Gadus morhua</i>
Small Atlantic cod (\leq 35 cm)	<i>Gadus morhua</i>
Large Greenland halibut (> 40 cm)	<i>Reinhardtius hippoglossoides</i>
Small Greenland halibut (\leq 40 cm)	<i>Reinhardtius hippoglossoides</i>
American plaice	<i>Hippoglossoides platessoides</i>
Flounders	Witch flounder <i>Glyptocephalus cynoglossus</i> , yellowtail flounder <i>Limanda ferruginea</i> , winter flounder <i>Pseudopleuronectes americanus</i>
Skates	Thorny skate <i>Amblyraja radiata</i> , smooth skate <i>Malacoraja senta</i> , winter skate <i>Leucoraja ocellata</i>
Redfish	<i>Sebastes fasciatus</i> , <i>S. mentella</i>

Table 1. Cont.

Group Name	Main species
Large demersal feeders	Black dogfish <i>Centroscyllium fabricii</i> , white hake <i>Urophycis tenuis</i> , marlin spike <i>Nezumia bairdi</i> , Atlantic halibut <i>Hippoglossus hippoglossus</i> , wolffish <i>Anarhichas</i> spp., common lumpfish <i>Cyclopterus lumpus</i> , haddock <i>Melanogrammus aeglefinus</i> , longfin hake <i>Urophycis chesteri</i> , large eelpouts (Zoarcidae), monkfish <i>Lophius americanus</i> , grenadiers (Macrouridae)
Small demersal feeders	Sculpins (Cottidae), small eelpouts (Zoarcidae), Atlantic hagfish (<i>Myxine glutinosa</i>), fourbeard rockling <i>Enchelyopus cimbrius</i> , cunner <i>Tautogolabrus adspersus</i> , gunnels (Pholidae), lumpsuckers <i>Eumicrotremus</i> spp., snailfishes (Liparidae), blennies (Stichaeidae), juvenile large demersals
Capelin	<i>Mallotus villosus</i> and Arctic cod ^b <i>Boreogadus saida</i>
Large pelagic feeders	Spiny dogfish <i>Squalus acanthias</i> , pollock <i>Pollachius virens</i> , silver hake <i>Merluccius bilinearis</i>
Piscivorous small pelagic feeders	Atlantic mackerel <i>Scomber scombrus</i> , piscivorous myctophids and other mesopelagics, short-finned squid <i>Illex illecebrosus</i> , piscivorous juvenile large pelagics
Planktivorous small pelagic feeders	Atlantic herring <i>Clupea harengus</i> , Atlantic argentine <i>Argentina silus</i> , planktivorous myctophids and other mesopelagics, planktivorous juvenile large pelagics, sand lance <i>Ammodytes</i> spp.
Shrimp	Northern shrimp <i>Pandalus borealis</i> , striped shrimp <i>P. montagui</i> , Arctic argid <i>Argis dentata</i> , Greenland shrimp <i>Eualus macilentus</i> , circumpolar eualid <i>E. gaimardii</i>
Large crabs (> 45 mm CW)	Snow crab <i>Chionoecetes opilio</i> , other non-commercial species (e.g., toad crabs <i>Hyas</i> spp.)
Small crabs (≤ 45 mm CW)	Snow crab <i>Chionoecetes opilio</i> , other non-commercial species (e.g., toad crabs <i>Hyas</i> spp.)
Echinoderms	Sand dollar <i>Echinarachnius parma</i> , sea urchin <i>Strongylocentrotus pallidus</i> , brittle star <i>Ophiura robusta</i>
Molluscs	Wedgeclam <i>Mesodesma deauratum</i> , propeller clam <i>Cyrtodaria siliqua</i>
Polychaetes	<i>Exogene hebes</i>
Other benthic invertebrates	Miscellaneous crustaceans, nematodes, other meiofauna

Table 1. Cont.

Group Name	Main species
Large zooplankton (> 5 mm)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians and ctenophores (jellyfish), mysids, tunicates > 5 mm, ichthyoplankton
Small zooplankton (< 5 mm)	Copepods (mainly <i>Calanus finmarchicus</i> , <i>C. hyperboreus</i> , and <i>Oithona similis</i>), tunicates < 5 mm, meroplankton
Phytoplankton	Diatom species such as <i>Chaetoceros affinis</i> , <i>Chaetoceros</i> spp., <i>Fragilariopsis oceanica</i> , <i>F. cylindrus</i> , <i>Leptocylindrus minimus</i> , <i>Thalassiosira bioculata</i> , <i>T. nordenskioldii</i> , <i>T. pacifica</i> , <i>T. punctigera</i> , and a mixture of autotrophic and mixotrophic organisms including Cryptophytes, dinoflagellates, Prasinophytes, Prymnesiophytes, and mixotrophic <i>Strombidium</i> spp.
Detritus	Sinking particulate organic matter including both large particles (consisting of animal carcasses and debris of terrigenous and coastal plants) and fine particles (mostly from planktonic organisms, including feces, moults, phytoplankton aggregates, and bacteria)

^a: Grey and harbour seals were grouped due to a weak trophic role in the earlier modelled time periods for harbour seals. Harbour seals accounted for 13% of this group's biomass.

^b: Included in the capelin group due to a combination of limited data and a weak trophic role.

Some groups such as large pelagic feeders and large demersal feeders are composite groups, where the species were aggregated on the basis of similarity in size and ecological role. Cod and Greenland halibut were each separated into two groups based on diet, size at first capture in fisheries, and size at maturity. Smaller fish prey mainly on invertebrates while larger fish feed mainly on fish. These changes tend to occur gradually with increasing length, but for this model it was assumed that the change occurs at 35 cm for cod (Lilly 1991) and 40 cm for Greenland halibut (Bowering and Lilly 1992). Due to a lack of data, we could not treat juveniles and adults separately for other fish species. Crabs were also each separated into two groups. Based on important differences in diet and vulnerability to predation (in particular cannibalism; crab prey ranged in size between 3.9 and 48.8 mm carapace width [CW]), and minimal carapace width of adult snow crabs (40 mm CW), crabs were separated into small (≤ 45 mm CW) and large crabs (> 45 mm CW) (Lovrich and Sainte-Marie 1997). Only large crabs are recruited to the fishery and consist almost exclusively of male snow crab, *Chionoecetes opilio* ≥ 95 mm CW.

Collecting the data

All parameter estimations were made within a collaborative framework, in which experts for the various functional groups were consulted. A considerable effort was expended to obtain input data in the study area and during the period of interest. However, information on several groups (e.g., forage species and benthic invertebrates) was sparse or non-existent for the area and period studied and was thus taken for the same area but for other time periods or from the literature for other areas and/or time periods. Based on these different sources of data (local and literature), we estimated the lower and upper limits of each input data used in inverse modelling.

Biomass

The biomass density (called biomass in this document) of a species (or group of species) was assumed to be constant for the 2003–2005 period modelled. The biomass of each box of the model was obtained directly or was estimated from similar ecosystems when it was not available for 4RS. This parameter is expressed in biomass per surface unit (i.e., tons wet weight km⁻²). Biomass was estimated from sequential population analysis or scientific trawl survey data for most groups.

An annual summer trawl survey for groundfish has been conducted since 1990 in the northern Gulf using a URI 81/114 trawl aboard the CCGS *Alfred Needler*. The sampling strategy consisted of a stratified random sampling into depth-based strata (Doubleday 1981). Weighted means were calculated to estimate the biomass in the area using the *PACES (Programme d'Analyse des Campagnes d'Échantillonnage Stratifiées)* software (Bourdages 2001). Note that biomass values estimated from this survey were considered “minimal trawlable biomasses” since the zones of the study area where the bottom is shallower than 20 fathoms were not sampled.

Biomass estimates for demersal fish and shrimp were based on catches in the annual summer bottom-trawl surveys. These survey estimates were converted to catchability-adjusted biomass based on catchability coefficients estimated by Harley and Myers (2001) and Savenkoff et al. (2004b). Length-specific corrections were applied to numbers-at-length data before they were converted to biomass estimates. In this way, we hope to lessen the impact of catchability on the biomass estimates and render data comparable between species.

Biomass estimates for several other model compartments were based on data from other surveys and population models (cetaceans, seabirds, crabs: population models; seals: updated version of the population model of Hammill and Stenson [2000]; Atlantic mackerel [*Scomber scombrus*]: derived from an egg production index; Atlantic herring [*Clupea harengus*]: from sequential population analysis). In other cases, biomass was based on densities reported from other survey estimates (zooplankton and phytoplankton), for other ecosystems (echinoderms, molluscs, polychaetes, and other benthic invertebrates), or was estimated by initial models to meet predator demands (capelin, small demersal feeders).

Standard deviations for biomass were based only on the variations in the point estimates for the three years in each period (i.e., error in the estimates themselves was not included in these standard deviations).

Catch

Annual landings for harvested species were estimated from the NAFO fisheries statistics (NAFO 2007) updated from related Canadian Science Advisory Secretariat science advisory reports. Standard deviations for catch were based only on the variations in the point estimates for the three years in each period (i.e., error in the estimates themselves was not included in these standard deviations).

Production

Production is the total amount of tissue produced in the population or community under study during a given time period (Christensen and Pauly 1992). It includes all living matter produced by a group (even if it is finally consumed, fished, or lost to other mortality) during the model period. In the northern Gulf of St. Lawrence model, it was assumed that there was no year-to-year change in biomass over the 2003–2005 time period and that emigration was zero. Thus production in this model is simply the biomass that is lost to natural mortality (predation, disease, and other natural causes of death) and fishing mortality. P/B is the ratio of production (P) to biomass (B). Absolute production is a flux expressed in biomass per surface unit per year (i.e., $\text{t km}^{-2} \text{yr}^{-1}$).

For most model compartments, estimates of production were obtained using the steady-state assumption that production equals total mortality. Direct estimates of total mortality (Z), based on a modified catch curve analysis of the survey data, were available only for large cod (Sinclair 2001) and American plaice (Morin et al. 2001). An estimate of production was then obtained by multiplying biomass by the annual mortality rate A ($A = 1 - e^{-Z}$, with Z being the instantaneous mortality rate according to Ricker [1980]). For most other model compartments, total mortality or production was assumed to be equivalent to the biomass multiplied by natural mortality (M), plus catch ($[B \times M] + C$) (Allen 1971). In these cases, a fixed rate of natural mortality was assumed based on life-history considerations, literature reports, or expert opinion. Minimum and maximum values for production were obtained by using ranges of catch and biomass values. In other cases, a range of production estimates was obtained by using a variety of methods to calculate production (seals, capelin, mackerel, herring, and shrimp) or based on a range of reported values for other areas (benthic invertebrates).

Consumption

Consumption is defined as the utilization of food by a group during the time period considered by the model (Christensen and Pauly 1993). Q/B is the ratio of consumption (Q) to biomass (B). Absolute consumption is a flux expressed in biomass per surface area per year (i.e., $\text{t km}^{-2} \text{yr}^{-1}$).

Consumption (Q) was estimated for each model compartment by multiplying biomass (B) by Q/B ratios reported in the literature, by dividing production (P) by gross growth efficiency (GE; the ratio of production to consumption) using the ranges in GE given by Christensen and Pauly (1992), or by using a consumption model (seals and seabirds). For each compartment, a

range in Q estimates was obtained based on 1) variation in reported Q/B ratios, 2) the range in possible GE, 3) variation in estimated biomass or production (mean \pm standard deviation), and/or 4) variation between the estimates obtained using the different methods described above. This range in Q estimates provided the minimum and maximum estimates used as constraints in inverse modelling. Also, we assumed that the fish species would eat at least as much food as their biomass ($Q/B \geq 1$).

Diet composition

Diet matrices were constructed using field data from the study area whenever possible. However, these data do not exist for some species. For these species, diet data were taken for the same area but for another time period or from the literature for other areas and/or time periods. Using all the available field samples or literature reports, the minimum and maximum values observed for each diet proportion were used as inputs for inverse modelling. Means and standard deviations were calculated either directly from the lower and upper limits when there was no information on numbers of stomachs (mean and SD of the two extreme values) or from the different diet proportions, which were weighted by the number of stomachs when stomach content analyses were given (mean and SD of all the point estimates). In the diet tables, empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts ($< 0.1\%$) or that this represented a potential trophic relation between prey and predator in other ecosystems or another period of time (equal to 0%). There was a large number of such values (95 of 361 flows) during the 2003–2005 period.

For Atlantic cod (*Gadus morhua*) and Greenland halibut (*Reinhardtius hippoglossoides*), in addition to diet composition, stomach fullness was estimated. Stomach fullness is shown as an indicator of feeding intensity when stomachs were collected. A stomach fullness index needs to take into account predator size. One method of doing this is to express stomach content mass as a percentage of fish mass. However many fish species, such as cod, display pronounced yearly cycles in condition. As a result, there is a large range of possible mass values for a fish of a given length, depending on sampling date. This can cause a large seasonal bias when this fullness index is used. Furthermore, predator length was measured more often than predator mass in the early years of our stomach database. Thus, the following fullness index was calculated:

$$(1) SFI_i = SCM_i * L_i^3 * 10^4$$

where SFI_i is the stomach fullness index for fish i , SCM_i is stomach content mass for fish i (in g), L_i is length of fish i (in cm). The allometric exponent 3 insures that length scales linearly with mass and the constant 10^4 brings this index on the same scale as expressing stomach content mass as a percent of predator mass; for most predators, a $SFI > 10$ represents a very full stomach. This index is widely used in the literature (e.g., Lilly 1991, Carruthers et al. 2005, Chabot et al. 2008).

FishBase

Occasionally, information was not available for some parameters. When this happened we referred to FishBase (Froese and Pauly 2002), which is a biological database developed at the International Centre for Living Aquatic Resources Management (ICLARM) in collaboration with FAO and other organizations. It includes information on fish species and is updated frequently with regards to information such as maximum size, growth parameters, natural mortality, and standardized diet composition (Froese and Pauly 2002). The Q/B ratio of different species was thus determined using FishBase (Life-history tool) based on water temperature, species mass, the aspect ratio of the caudal fin of fish, and the general diet composition.

RESULTS: DATA GATHERING AND SYNTHESIS

In this section, we describe each functional group of the northern Gulf of St. Lawrence ecosystem and give the respective estimates of biomass, production, consumption, and diet composition that are used as inputs for modelling.

Cetaceans: mysticeti and odontoceti

Background

The northern Gulf of St. Lawrence is dominated by boreal cetaceans ranging from large and medium-sized mysticetes and odontocetes to small odontocetes such as porpoises and dolphins (Kingsley and Reeves 1998). Minke (*Balaenoptera acutorostrata*), fin (*Balaenoptera physalus*), long-finned pilot (*Globicephala melas*), and humpback (*Megaptera novaeangliae*) whales are the most abundant species among the large and medium whales. The harbour porpoise (*Phocoena phocoena*) is the most abundant of the small dolphins in the Gulf while white-sided dolphins (*Lagenorhynchus acutus*) and white-beaked dolphins (*Lagenorhynchus albirostris*) also occur in this area (Kingsley and Reeves 1998). The cetacean survey of the Gulf of St. Lawrence (Kingsley and Reeves 1998) covered 221,950 km², so we used this inventory area to calculate the parameters for this group instead of the value habitually used for the other groups (the sampling area for divisions 4RS).

Based on diet and body mass, the cetacea were separated into two groups: the mysticeti (baleen whales) and the odontoceti (toothed whales). For the species included in the model, mysticeti mean weights varied between 5.6 (minke whale) and 38.5 t (fin whale) while odontoceti mean weights ranged between 0.05 and 0.22 t (references are listed on the next page).

Catch

Canada ceased commercial whaling in 1972 and there has been no hunt since that time in 4RS. However, information from a questionnaire survey conducted in 2000 and 2001 in the Gulf (4RST) indicated an annual average incidental catch from fishing gear of 1,030 odontoceti

harbour porpoises (Lesage et al. 2003). This is equivalent to a catch of 51.5 tons within a 244,792 km² sampling area ($2.10 \times 10^{-4} \pm 9.04 \times 10^{-5}$ t km⁻² yr⁻¹). Due to the lack of reliable information on incidental catch in the 2003–2005 period, we used the previous values as modelling inputs. The final solution of inverse modelling (hereafter termed “inverse solution”) estimated a catch of 2.06×10^{-4} t km⁻² yr⁻¹ for odontoceti.

Biomass

Aerial survey estimates of cetacean abundance in the Gulf of St. Lawrence, not corrected for visibility bias, are available for the summer of 1995 (Kingsley and Reeves 1998). The area of the strata corresponding to the northern Gulf covers 144,468 km². The density in this zone is applied to the present study zone. These estimates were adjusted by a factor of 1.09 to account for animals that were potentially visible to the observers but were not seen (Marsh and Sinclair 1989) and by a factor of 2.27 to account for animals missed owing to water turbidity and diving behaviour (Marsh and Sinclair 1989). These adjustments resulted in abundance estimates of 297 humpback whales, 990 fin whales, 2,128 minke whales, 3,019 long-finned pilot whales, 21,427 harbour porpoises, 17,419 white-sided dolphins, and 6,532 white-beaked dolphins. Other whales, like blue whales for instance, were present in the survey of the Gulf of St. Lawrence but were seen too infrequently to allow any estimation of their biomass.

Mean body mass taken from the literature was 31 t for humpback whales (averaged from Hay [1985], Martin [1990], and Kenney et al. [1997]); 38.5 t for fin whales, 5.6 t for minke whales, 1.4 t for long-finned pilot whales, and 0.05 t for harbour porpoises (averaged from Lien [1985], Martin [1990], and Kenney et al. [1997]); 0.13 t for white-sided dolphins (Sergeant et al. 1980); and 0.217 t for white-beaked dolphins (Ridgway and Harrison 1999). To calculate biomass in the 2003–2005 period from the reference time period (1995), we used a population growth rate of 6.5% for humpback whales (Barlow and Clapham 1997), 6.7% for fin whales (Bundy et al. 2000), 6.7% for minke whales (Bundy et al. 2000), 4.0% for long-finned pilot whales (Waring et al. 1999), 9.0% for harbour porpoises (Caswell et al. 1998), 2.0% for white-sided dolphins (Heise 1997), and 2.0% for white-beaked dolphins (Heise 1997). For harbour porpoises, an annual incidental catch of 608 individuals was also used (Lesage et al. 2003). Assuming a residence time of 180 days for all whales within the potential area of Kingsley and Reeves (1998) (144,468 km²), the average annual biomass was 52,292 tons or 0.362 ± 0.160 t km⁻² for mysticeti and 6,069 tons or 0.042 ± 0.018 t for odontoceti.

Production

Because there is no information on total mortality for cetaceans, production was assumed to be equivalent to the biomass multiplied by natural mortality (M), plus catch (Allen 1971). Natural mortality for a combination of cetaceans was estimated to be 0.068 for mysticeti (Ohsumi 1979, Tanaka 1990) and 0.146 for odontoceti (Ohsumi 1979). No catch has been reported for mysticeti while the mean annual catch for odontoceti used was 2.10×10^{-4} t km⁻² yr⁻¹. We used the coefficients of variation for biomass (44% and 43%, respectively, for mysticeti and odontoceti) to

estimate the standard deviations for production. This resulted in a total annual production of $0.021 \pm 0.011 \text{ t km}^{-2} \text{ yr}^{-1}$ (range: $0.014\text{--}0.035 \text{ t km}^{-2} \text{ yr}^{-1}$) for mysticeti and $0.006 \pm 0.003 \text{ t km}^{-2} \text{ yr}^{-1}$ (range: $0.004\text{--}0.009 \text{ t km}^{-2} \text{ yr}^{-1}$) for odontoceti. The inverse solution estimated a production of $0.017 \text{ t km}^{-2} \text{ yr}^{-1}$ (P/B of 0.05 yr^{-1}) for mysticeti and $0.004 \text{ t km}^{-2} \text{ yr}^{-1}$ (P/B of 0.09 yr^{-1}) for odontoceti.

Consumption

The daily consumption by cetaceans was calculated using:

$$(2) R = 0.1W^{0.8}$$

where R is the daily ration for an individual (in kg) and W is the mean body mass in (kg) (Trites et al. 1997). Assuming a residence time of 180 days, the annual consumption by species was $0.256 \text{ t km}^{-2} \text{ yr}^{-1}$ for humpback whales, $1.032 \text{ t km}^{-2} \text{ yr}^{-1}$ for fin whales, and $0.474 \text{ t km}^{-2} \text{ yr}^{-1}$ for minke whales. This gives a mean annual consumption of $1.762 \pm 0.779 \text{ t km}^{-2} \text{ yr}^{-1}$ (range: $0.983\text{--}2.541 \text{ t km}^{-2} \text{ yr}^{-1}$) for mysticeti using the coefficient of variation for mysticeti biomass (44%) to estimate the standard deviation for consumption. Gross growth efficiency ($GE = P/Q$) ranges between 0.1 and 1% for marine mammals (Christensen and Pauly 1992). Based on the previous total annual production ($0.025 \text{ t km}^{-2} \text{ yr}^{-1}$) and the GE limits, we obtained two other consumption values of 2.458 and $24.577 \text{ t km}^{-2} \text{ yr}^{-1}$. The value based on the lower GE limit (0.1%) was not realistic; i.e., 10-fold the value based on GE limit of 1%. So the resulting consumption range for mysticeti was 0.983 to $2.541 \text{ t km}^{-2} \text{ yr}^{-1}$ (mean consumption value: $1.762 \pm 1.102 \text{ t km}^{-2} \text{ yr}^{-1}$). The inverse solution estimated a consumption for mysticeti of $1.920 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a Q/B of 5.306 yr^{-1} .

For odontoceti, assuming a residence time of 180 days, the annual consumption by species was $0.176 \text{ t km}^{-2} \text{ yr}^{-1}$ for long-finned pilot whales, $0.108 \text{ t km}^{-2} \text{ yr}^{-1}$ for harbour porpoises, $0.127 \text{ t km}^{-2} \text{ yr}^{-1}$ for white-sided dolphins, and $0.072 \text{ t km}^{-2} \text{ yr}^{-1}$ for white-beaked dolphins. This gives a mean annual consumption of $0.483 \pm 0.205 \text{ t km}^{-2} \text{ yr}^{-1}$ (range: $0.278\text{--}0.688 \text{ t km}^{-2} \text{ yr}^{-1}$) for odontoceti using the coefficient of variation for odontoceti biomass (43%) to estimate the standard deviation for consumption. Gross growth efficiency ($GE = P/Q$) ranges between 0.1 and 1% for marine mammals (Christensen and Pauly 1992). Based on the previous total annual production ($0.006 \text{ t km}^{-2} \text{ yr}^{-1}$) and the GE limits, we obtained two other consumption values of 0.633 and $6.327 \text{ t km}^{-2} \text{ yr}^{-1}$. The value based on the lower GE limit was not realistic, so the resulting consumption range for odontoceti was 0.278 and $0.688 \text{ t km}^{-2} \text{ yr}^{-1}$ (mean consumption value: $0.483 \pm 0.290 \text{ t km}^{-2} \text{ yr}^{-1}$). The inverse solution estimated a consumption for odontoceti of $0.421 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a Q/B of 10.023 yr^{-1} .

Diet composition

Unfortunately, there are few quantitative descriptions of diet for cetaceans. Where the literature refers to prey using terms such as "preponderant" or "predominant," it was assumed that they make up at least 75% of consumption by mass. If other prey were reported, remaining

consumption was divided equally among them. Based on the literature, the following diets were used in the analysis:

- Humpback whales: capelin, sand lance, squid, and euphausiids (Mitchell 1973);
- Fin whales: capelin, sand lance, herring, and euphausiids (Mitchell 1975);
- Minke whales: capelin, small cod, herring, squid, and euphausiids (Horwood 1990);
- Long-finned pilot whales: squid, juvenile cod, and capelin (Lien 1985);
- Harbour porpoises: capelin, herring, redfish, mackerel, cod, squid, and sand lance (Fontaine et al. 1994);
- White-sided dolphins: herring, squid, smelt, silver hake, and crustaceans (Katona et al. 1978);
- White-beaked dolphins: cod, whiting, mackerel, and cephalopods (Santos et al. 1994).

To calculate the overall proportion of each prey item by mass, total consumption by prey type was first calculated and overall proportions for mysticeti and odontoceti weighted according to the consumption of each cetacean species (Table 3).

Table 2. Diet compositions (%) for mysticeti (baleen whales) and odontoceti (toothed whales) used in modelling. Est: diet estimates from the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Prey	Mysticeti					Odontoceti				
	Mean	±SD ^a	Min	Max	Est	Mean	±SD ^a	Min	Max	Est
Large cod	0.0	0.0	0.0	0.0	0.0	1.1	1.6	0.0	2.6	1.5
Small cod	1.3	2.1	0.0	3.4	0.0	3.1	4.8	0.0	7.9	0.2
Large Green. halibut										
Small Green. halibut										
American plaice	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Flounders										
Skates										
Redfish	0.0	0.0	0.0	0.0	0.0	1.3	2.0	0.0	3.3	2.9
Large demersals	0.0	0.0	0.0	0.0	0.0	2.1	3.4	0.0	5.5	4.8
Small demersals	0.0	0.0	0.0	0.0	0.0	12.1	15.2	0.0	27.4	6.1
Capelin	53.0	65.7	0.0	100.0	53.3	9.0	11.1	0.0	20.0	18.5
Large pelagics	0.0	0.0	0.0	0.0	0.0	1.5	2.6	0.0	4.1	0.1
Pisci. small pelagics	3.9	5.8	0.0	9.8	0.9	58.1	85.9	0.0	100.0	42.4
Plank. small pelagics	11.6	14.4	0.0	26.0	5.2	10.9	13.5	0.0	24.3	22.6
Shrimp	0.0	0.0	0.0	0.0	0.0	0.9	0.9	0.0	1.7	0.9
Large crabs										
Small crabs										
Echinoderms										
Molluscs										
Polychaetes										
Other bent. inver.										
Large zooplankton	30.0	34.0	0.0	64.0	40.6	0.0	0.0	0.0	0.0	0.0
Small zooplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phytoplankton										
Detritus										
Total	100.0		0.0	203.2	100.0	100.0		0.0	196.9	100.0
TRN	13					13				

^a: For these two groups, all the proportions of prey in the diet composition were available only as point estimates. SD was then calculated as $DC_{x \rightarrow y}^{obs} * CV(DC_{x \rightarrow u}^{obs})_{mean}$ ($SD = CV * Mean$), with $DC_{x \rightarrow y}^{obs}$ representing the proportion of prey x consumed by the mysticeti or odontoceti group and $CV(DC_{x \rightarrow u}^{obs})_{mean}$ representing the average of all coefficients of variation of the proportion of prey x consumed by the other groups u of the modelled ecosystem. Min = mean – SD, Max = mean + SD.

Seals

Background

Four species of pinnipeds occur in the Gulf of St. Lawrence: harp seals (*Pagophilus groenlandica*), grey seals (*Halichoerus grypus*), hooded seals (*Cystophora cristata*), and harbour seals (*Phoca vitulina*). Harp and grey seals are the most abundant pinnipeds in the Gulf. The harp seal is the most abundant pinniped in Atlantic Canada and usually summers in the Canadian Arctic or northwest Greenland before returning south to overwinter in Canadian Atlantic waters. Reproduction occurs in March on pack ice in the Gulf of St. Lawrence (Gulf herd) and off southern Labrador (Front herd). In the Gulf, animals whelp in two areas: off the lower North Shore and near the Îles-de-la-Madeleine (Sergeant 1991). During the 2003–2005 period, the northwest Atlantic population was estimated to be 5,719,586 (M. Hammill, unpublished data), with an average of 2.5% of the pups, 2.5% of juveniles, and 4.1% of the adults found in the northern Gulf of St. Lawrence (Hammill and Stenson 2000).

Hooded seals, which are larger than harp seals, are the least abundant pinniped within the study area, with an average population of 19,287 individuals for 2003–2005 in the Gulf of St. Lawrence, of which 6,982 or 36.2% would have been in divisions 4RS (Hammill and Stenson 2000, M. Hammill, unpublished data). In the northwest Atlantic, most pups are born in March on pack ice off northeast Newfoundland, with smaller whelping concentrations located in Davis Strait and the Gulf of St. Lawrence. After leaving the whelping patch in late March, adults from the Gulf of St. Lawrence move to the northern Gulf where they remain until mid-May, after which they return to Greenland. Hooded seals have been protected in the Gulf since 1972 (Hammill et al. 1997).

The grey seal is slightly smaller than the hooded seal. Major breeding colonies in eastern Canada are located on Sable Island and in the southern Gulf of St. Lawrence (Mansfield and Beck 1977). After breeding, both juveniles and adults disperse widely over eastern Canada. Large numbers are known to feed in the northern Gulf of St. Lawrence, which makes it the second most abundant pinniped of the zone (Hammill and Stenson 2000). The Gulf herd population was estimated to average 51,470 individuals in 2003–2005, whereas the Sable Island herd averaged 213,676 individuals (M. Hammill, unpublished data). It has been estimated that 33.7% of the Gulf herd and 7.9% of the Sable Island herd are found in divisions 4RS for about 6 months of the year (Hammill and Stenson 2000).

Harbour seals are found throughout eastern Canada (Boulva and McLaren 1979), occurring in small groups dispersed along coastal areas (Lesage et al. 1995). Harbour seal abundance in Atlantic Canada has never been evaluated by direct survey. Based on questionnaires sent to fisheries officers, Boulva and McLaren (1979) estimated about 13,000 animals in eastern Canada.

Based on an estimated annual population rate of increase for this species (5.7%), the average population was 49,701 for 2003–2005 (M. Hammill, unpublished data), with 26.4% of the animals situated in the northern Gulf (Hammill and Stenson 2000).

For the purpose of this study, grey and harbour seals were grouped due to a combination of limited data and a weak trophic role in the earlier modelled time periods for harbour seals.

Catch

Commercial catches (total numbers) for harp, grey, and hooded seals are reported in the Atlantic resource management landing reports (DFO 2003a). For harp seals, catches in number (66,179 in 2003; 106,780 in 2004; 103,116 in 2005) from the west coast of Newfoundland and Québec's North Shore were divided into pups (young of the year) and animals one year and older (Sjare et al. 1996). Numbers-at-age were multiplied by mean mass-at-age (Hammill and Stenson 2000) to obtain total catches in tons. For harp seals, the mean annual catch for 2003–2005 was estimated at $3.21 \times 10^{-2} \pm 7.67 \times 10^{-3} \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a catch of $2.35 \times 10^{-2} \text{ t km}^{-2} \text{ yr}^{-1}$ for this group.

Hooded seals have been protected in the Gulf since 1972 (Hammill et al. 1997). Thus, there is no catch value constrained in the model.

There is a small commercial hunt for grey seals in Canadian waters. This species was hunted for bounty until 1992, when the hunt was eliminated (Hammill et al. 1998). Scientific collection results in the removal of grey seals, with an estimated mean annual catch of $1.95 \times 10^{-5} \pm 3.37 \times 10^{-5} \text{ t km}^{-2} \text{ yr}^{-1}$ for the study period. Even though harbour seals have been protected since 1976 (Boulva and McLaren 1979), some losses may have occurred through by-catch by commercial fisheries. However, there are no data available to assess this loss and catch was assumed to be negligible. The total mean annual catch for the grey and harbour seals was estimated to be $1.95 \times 10^{-5} \pm 3.37 \times 10^{-5} \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a catch of $2.93 \times 10^{-5} \text{ t km}^{-2} \text{ yr}^{-1}$ for this group.

Biomass

Biomass was estimated by multiplying abundance by mean mass-at-age. The number of seals in each age class was obtained from an updated version of the population model of Hammill and Stenson (2000). Biomass was adjusted for residence time in 4RS (Hammill and Stenson 2000), resulting in mean annual biomass estimates for the 2003–2005 period of $0.151 \pm 0.003 \text{ t km}^{-2}$ for harp seals, $0.007 \pm 0.000 \text{ t km}^{-2}$ for hooded seals, and $0.047 \pm 0.003 \text{ t km}^{-2}$ for grey and harbour seals.

Production

The P/B ratio for each group was estimated by dividing the pup biomass by the population biomass (minimum value) for the northern Gulf of St. Lawrence as reported in an updated version of the population model of Hammill and Stenson (2000) for the 2003–2005 period. The P/B ratios

were 0.073 yr^{-1} for harp seals, 0.049 yr^{-1} for hooded seals, 0.086 yr^{-1} for grey seals, and 0.071 yr^{-1} for harbour seals. Multiplying these P/B ratios by mean biomass for each species resulted in production values of $0.011 \pm 0.000 \text{ t km}^{-2} \text{ yr}^{-1}$ for harp seals, $0.0004 \pm 0.0000 \text{ t km}^{-2} \text{ yr}^{-1}$ for hooded seals, and $0.004 \pm 0.000 \text{ t km}^{-2} \text{ yr}^{-1}$ for grey and harbour seals.

Production was also estimated by adding the annual mass gain for each age class in the population to the mass of pups. Mass at age was obtained from Chabot and Stenson (2002) and Leblanc (2003) for harp seals and hooded seals, respectively. An updated version of the population model of Hammill and Stenson (2000) provided the information for grey and harbour seals. In the 2003–2005 period, this resulted in production values of $0.026 \text{ t km}^{-2} \text{ yr}^{-1}$ for harp seals, $0.0007 \text{ t km}^{-2} \text{ yr}^{-1}$ for hooded seals, and $0.010 \text{ t km}^{-2} \text{ yr}^{-1}$ for grey and harbour seals.

Finally, the resulting upper and lower limit ranges were 0.011 to $0.026 \text{ t km}^{-2} \text{ yr}^{-1}$ (mean: $0.018 \pm 0.010 \text{ t km}^{-2} \text{ yr}^{-1}$) for harp seals, 0.0004 to $0.0007 \text{ t km}^{-2} \text{ yr}^{-1}$ (mean: $0.0005 \pm 0.0003 \text{ t km}^{-2} \text{ yr}^{-1}$) for hooded seals, and 0.004 to $0.010 \text{ t km}^{-2} \text{ yr}^{-1}$ (mean: $0.007 \pm 0.004 \text{ t km}^{-2} \text{ yr}^{-1}$) for grey and harbour seals. For harp seals, mortality through total removals (i.e., catch; $0.032 \text{ t km}^{-2} \text{ yr}^{-1}$) is greater than production ($0.018 \text{ t km}^{-2} \text{ yr}^{-1}$), thus biomass will decrease and we have to include a negative change in biomass (ΔB_i) in the mass balance equation of harp seals.

$$(3) P_y - \sum_u Pr_{y \rightarrow u} - MO_y - EX_y = -\Delta B_y + \varepsilon$$

or

$$(4) P_y + \Delta B_y = \sum_u Pr_{y \rightarrow u} + MO_y + EX_y + \varepsilon$$

Production of harp seals (P_y) plus the net change in biomass (ΔB_i) were equal to the biomass lost to predation ($\sum_u Pr_{y \rightarrow u} = 0$), other mortality causes (MO_y), total removals (EX_y), and a residual term (ε). Other mortality causes (i.e., 1-EE) could thus vary between 5% and 100% of P_y . Here, harp seals were heavily harvested, leaving few individuals to die of other causes (e.g., $MO_y = 5\% P_y$). Accordingly, a negative change in biomass of $-0.015 \pm 0.008 \text{ t km}^{-2} \text{ yr}^{-1}$ could be estimated using the coefficient of variation for production ($0.010/0.018 = 57\%$). The inverse solution estimated production values of $0.016 \text{ t km}^{-2} \text{ yr}^{-1}$ ($P/B = 0.11 \text{ yr}^{-1}$) for harp seals (with a mean net change in biomass of $-0.008 \text{ t km}^{-2} \text{ yr}^{-1}$), $0.0007 \text{ t km}^{-2} \text{ yr}^{-1}$ ($P/B = 0.10 \text{ yr}^{-1}$) for hooded seals, and $0.004 \text{ t km}^{-2} \text{ yr}^{-1}$ ($P/B = 0.09 \text{ yr}^{-1}$) for grey and harbour seals.

Consumption

The total annual consumption of prey by each seal species in the study area was estimated from an updated version of the consumption model of Hammill and Stenson (2000) that also corrected the estimates from their residence time. The mean annual consumption values were $0.642 \pm 0.012 \text{ t km}^{-2} \text{ yr}^{-1}$ ($0.629\text{--}0.654 \text{ t km}^{-2} \text{ yr}^{-1}$) for harp seals, $0.089 \pm 0.002 \text{ t km}^{-2} \text{ yr}^{-1}$ ($0.087\text{--}0.091 \text{ t km}^{-2} \text{ yr}^{-1}$) for hooded seals, and $0.181 \pm 0.015 \text{ t km}^{-2} \text{ yr}^{-1}$ ($0.166\text{--}0.195 \text{ t km}^{-2} \text{ yr}^{-1}$) for grey and harbour seals.

Based on the mean annual production estimated (see above) and the upper GE limit (1%; values based on the lower GE limit of 0.1% were not realistic; i.e., 10-fold the value based on GE limit of 1%), we obtained other consumption values: $1.838 \text{ t km}^{-2} \text{ yr}^{-1}$ for harp seals, $0.055 \text{ t km}^{-2} \text{ yr}^{-1}$ for hooded seals, and $0.679 \text{ t km}^{-2} \text{ yr}^{-1}$ for grey and harbour seals. Finally, based on these different values, we estimated the lower and upper consumption limits used as constraints in inverse modelling. The resulting mean consumption values of each upper and lower limit range were $1.234 \pm 0.855 \text{ t km}^{-2} \text{ yr}^{-1}$ for harp seals, $0.073 \pm 0.026 \text{ t km}^{-2} \text{ yr}^{-1}$ for hooded seals, and $0.423 \pm 0.362 \text{ t km}^{-2} \text{ yr}^{-1}$ for grey and harbour seals. The inverse solution estimated consumption values of $1.644 \text{ t km}^{-2} \text{ yr}^{-1}$ ($Q/B = 10.907 \text{ yr}^{-1}$) for harp seals, $0.084 \text{ t km}^{-2} \text{ yr}^{-1}$ ($Q/B = 11.514 \text{ yr}^{-1}$) for hooded seals, and $0.407 \text{ t km}^{-2} \text{ yr}^{-1}$ ($Q/B = 8.631 \text{ yr}^{-1}$) for grey and harbour seals.

Diet composition

For harp seals, diet information was available for pups ($n = 184$), juveniles (i.e., age 1–4; $n = 94$), and adults ($n = 51$) in the northern Gulf during 1998–2001 (M. Hammill, unpublished data). The different diet proportions of the final diet were weighted by the biomass proportion of each class (5%, 17%, and 78%, respectively, for pups, juveniles, and adults). According to these diets, the main prey species were, in order of importance, Atlantic herring (planktivorous small pelagic feeders), capelin, small demersals, small Atlantic cod, and shrimp (Table 3).

There was no local hooded seal diet available for the 2003–2005 period in the northern Gulf. We used the diet composition estimated by Savenkoff et al. (2005) in the northern Gulf for the 2000–2002 period. This diet composition was based on different studies from the Gulf of St. Lawrence and the Newfoundland–Labrador Shelf (Lawson et al. 1993, Ross 1993, Hammill et al. 1997, Bundy et al. 2000, Hammill and Stenson 2000). Other information about this species was based on inshore and offshore samples from NAFO divisions 2J3KL and the west coast of Newfoundland collected from 1993–2000 (Stenson and Hammill, unpublished data). According to these studies, the main prey species were redfish, Atlantic cod, Greenland halibut, piscivorous small pelagic feeders (e.g., mackerel, squid), flounders, and planktivorous small pelagic feeders (e.g., herring) (Table 3).

For grey seals, diet information was available for pups ($n = 1$), juveniles (i.e., age 1–4; $n = 5$), and adults ($n = 18$) in the northern Gulf in 2004 (M. Hammill, unpublished data). The different diet proportions of the overall grey seal diet were weighted by the biomass proportion of each class (9%, 22%, and 69%, respectively, for pups, juveniles, and adults). We also used the study of Hammill et al. (2007) based on seals collected between 1985 and 2004 in the Gulf of St. Lawrence and around Newfoundland (east coast of Newfoundland: $n = 25$, south coast: $n = 24$, and west coast: $n = 70$). The different prey proportions of the final diet were weighted by seal numbers in each area. According to these studies, the main prey species were planktivorous small pelagic feeders (e.g., herring), Atlantic cod, small demersals, large demersals, and large pelagics. The harbour seal diet composition was examined in two inshore habitats of Atlantic Canada (lower Bay of Fundy and the northeastern coast of Nova Scotia) between 1988 and 1992 (Bowen and Harrison 1996). For the 250 food-containing stomachs examined, the major prey were Atlantic herring, squid, pollock (*Pollachius virens*), and Atlantic cod. We obtained upper and lower limits resulting from these different diet studies. These upper and lower limits were then weighted according to each seal species' consumption in order to calculate the overall proportion

of each prey item by mass for the grey/harbour seal group. The resulting diet composition is shown in Table 4.

Table 3. Diet compositions (%) for harp and hooded seals used in modelling. Est: diet estimates from the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Prey	Harp seals					Hooded seals				
	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod	3.9	2.3	0.0	14.3	5.0	11.3	16.5	0.5	21.4	13.1
Small cod	8.5	3.4	0.0	29.6	2.0	11.2	16.1	0.5	21.3	1.5
Large Green. halibut	0.5	0.7	0.0	3.3	1.5	5.6	5.1	0.0	24.4	7.0
Small Green. halibut	0.5	0.7	0.0	3.3	1.5	12.9	34.0	0.0	48.9	11.2
American plaice	1.3	1.9	0.0	12.5	5.9	1.8	3.1	0.0	8.6	2.1
Flounders	0.5	0.7	0.0	3.5	0.3	6.7	21.9	0.0	30.6	5.5
Skates	0.0	0.0	0.0	0.0	0.0					
Redfish	1.4	1.3	0.0	10.8	5.0	25.5	17.1	4.4	68.7	48.7
Large demersals	4.4	2.5	0.0	20.4	1.2	1.0	2.1	0.0	2.4	0.6
Small demersals	8.6	4.2	1.4	30.6	1.4	2.5	8.6	0.0	12.0	0.1
Capelin	24.2	11.4	0.4	73.5	39.1	4.3	10.3	0.4	16.1	3.4
Large pelagics	2.3	1.4	0.0	10.0	0.0	0.1	0.5	0.0	0.8	0.1
Pisci. small pelagics	0.6	0.8	0.0	4.0	0.1	9.4	9.2	0.0	35.4	2.4
Plank. small pelagics	31.8	12.4	2.9	83.3	13.7	6.0	11.2	0.0	14.7	2.5
Shrimp	7.8	7.8	0.0	38.2	14.0	0.0	0.0	0.0	0.0	0.0
Large crabs	0.1	0.4	0.0	1.8	0.1					
Small crabs	0.1	0.4	0.0	1.8	0.1					
Echinoderms										
Molluscs	0.2	0.6	0.0	2.3	1.0					
Polychaetes										
Other bent. inver.	0.0	0.0	0.0	0.0	0.0	1.8	6.8	0.0	7.0	1.7
Large zooplankton	3.3	5.7	0.0	38.3	8.0	0.0	0.0	0.0	0.1	0.0
Small zooplankton	0.0	0.0	0.0	0.0	0.0					
Phytoplankton										
Detritus										
Total	100.0		4.6	381.5	100.0	100.0		5.9	312.6	100.0
TRN	21					16				

Table 4. Diet compositions (%) for grey and harbour seal group used in modelling. Est: diet estimates from the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Prey	Grey/harbour seals				
	Mean	± SD	Min	Max	Est
Large cod	7.5	22.8	0.2	32.5	9.1
Small cod	7.5	22.8	0.3	32.5	2.0
Large Green. halibut	0.7	4.9	0.0	7.0	4.4
Small Green. halibut	0.7	4.9	0.0	7.0	4.8
American plaice	1.8	12.5	0.0	17.6	0.3
Flounders	1.8	16.8	0.2	24.0	0.7
Skates	0.0	0.0	0.0	0.0	0.0
Redfish	2.8	27.2	0.1	38.5	9.3
Large demersals	5.2	13.7	0.3	19.8	1.1
Small demersals	7.2	27.8	0.4	39.7	0.4
Capelin	5.1	31.7	0.8	45.6	34.6
Large pelagics	4.9	11.8	1.1	17.8	1.1
Pisci. small pelagics	6.1	22.4	3.9	35.6	3.9
Plank. small pelagics	43.7	61.4	4.4	91.3	15.4
Shrimp	4.4	15.8	0.8	23.1	12.4
Large crabs	0.1	1.3	0.0	1.8	0.1
Small crabs	0.1	1.3	0.0	1.8	0.1
Echinoderms					
Molluscs	0.0	0.0	0.0	0.0	0.0
Polychaetes					
Other bent. inver.	0.0	0.0	0.0	0.0	0.0
Large zooplankton	0.1	2.0	0.0	2.9	0.1
Small zooplankton					
Phytoplankton					
Detritus					
Total	100.0		12.7	438.7	100.0
TRN	20				

Seabirds

Background

In the northern Gulf of St. Lawrence, 64.5% of seabirds are estimated to be found inshore while 35.5% are distributed offshore (Cairns et al. 1991). Inshore seabirds breed in a large number of smaller colonies dispersed along the coastline while offshore species breed in a small number of large colonies (Lack 1967). The main inshore species breeding in the region are the double-crested cormorant (*Phalacrocorax auritus*), ring-billed gull (*Larus delawarensis*), herring gull (*Larus argentatus*), great black-backed gull (*Larus marinus*), common tern (*Sterna hirundo*), Arctic tern (*Sterna paradisaea*), and black guillemot (*Cepphus grylle*). The main offshore species that breed in the region are the northern gannet (*Morus bassanus*), black-legged kittiwake (*Rissa tridactyla*), common murre (*Uria aalge*), razorbill (*Alca torda*), Atlantic puffin (*Fratercula arctica*), and Leach's storm-petrel (*Oceanodroma leucorhoa*).

Catch/anthropogenic mortality

There are three primary sources of anthropogenic mortality for seabirds in the region: 1) by-catch in fishing gear, 2) hunting, and 3) oil pollution (Montevecchi and Tuck 1987). In the northern Gulf, a few species of seabirds such as ducks and guillemots are hunted for food along Québec's North Shore. Considerable numbers of seabirds (mostly alcids, i.e., murre and puffins, but also others, e.g., gannets) are caught as by-catch in fishing gear. Bundy et al. (2000) assumed that mortality coming from hunting, by-catch, and maritime traffic amounted to $1 \times 10^{-3} \text{ t km}^{-2}$ per year. On the basis of information for seabirds from Newfoundland (NAFO divisions 2J3KL) (Bundy et al. 2000), we estimated a catch rate ($1 \times 10^{-3} \text{ t km}^{-2} \text{ yr}^{-1}$ divided by the seabird biomass, 0.012 t km^{-2}) for the Newfoundland ecosystem and we applied it to the divisions 4RS. It totalled $2.55 \times 10^{-4} \text{ t km}^{-2} \text{ yr}^{-1}$ of seabirds being removed annually from the study area through anthropogenic mortality. The inverse solution estimated a catch of $1.58 \times 10^{-4} \text{ t km}^{-2} \text{ yr}^{-1}$.

Biomass

Unlike the open Atlantic coast of Canada, the Gulf of St. Lawrence is not frequented by large numbers of trans-oceanic and trans-equatorial migrants (Brown 1986). Thus, population estimates based on counts of breeding colonies can be used (Cairns et al. 1990). Data on body mass and population estimates for various seabirds were derived from Chapdelaine (Environment Canada, Migratory Birds Division, Sainte-Foy, Québec, unpublished data). In order to estimate biomass density, we assumed that seabirds were distributed uniformly throughout NAFO divisions 4RST. Consequently, biomass was determined by taking the number of birds multiplied by their respective biomass and divided by the whole 4RST bird inventory area ($214,000 \text{ km}^2$) instead of the value usually used for the other groups (the sampling area for divisions 4RS). Population surveys typically enumerated the number of breeding pairs. As such, it was necessary to estimate the number of nestlings and non-breeding birds. For species that breed within NAFO

divisions 4RST, population estimates (Table 5) were calculated as follows (G. Chapdelaine, unpublished data):

$$(5) \text{ Population estimate} = \begin{array}{l} \text{breeders} \\ + \text{nestlings} \\ + \text{non-breeders} \end{array}$$

$$(6) \text{ Population estimate (offshore species)} = \begin{array}{l} \text{breeding pairs} \times 2 \\ + (0.6 \times \text{breeding pairs}) \\ + (0.8 \times \text{breeding pairs}) \end{array}$$

or

$$(7) \text{ Population estimate (inshore species)} = \begin{array}{l} \text{breeding pairs} \times 2 \\ + (0.6 \times \text{breeding pairs}) \\ + (1.0 \times \text{breeding pairs}) \end{array}$$

The total biomass estimate for the 4RS study area is 859 t or 0.004 t km^{-2} . Other information about these species was based on a study for the North Atlantic (Barrett et al. 2006). These authors estimated a seabird biomass of 2100 t or 0.002 t km^{-2} in the Gulf of St Lawrence and Scotian Shelf (total area: 10^6 km^2). Accordingly, the mean biomass for the 4RS area was $0.003 \pm 0.001 \text{ t km}^{-2}$.

Table 5. Approximate period of occupation, population size, average body mass, and biomass for the main species of seabirds that breed within the study area (NAFO divisions 4RS) or that breed primarily or completely outside but occur in the study area or are nestlings. Note that the shaded section indicates inshore seabirds while the unshaded section corresponds to offshore seabirds.

Species	Period of occupation	Population (numbers) of breeders	Population (numbers) of non-breeders and nestlings	Individual mass (kg)	Adjusted average biomass (t)
Great cormorant	Apr-Oct	4,968	3,478	2.25	11.085
Double-crested cormorant	Apr-Oct	78,000	54,600	1.67	205.148
Ring-billed gull	Apr-Oct	66,784	53,427	0.50	35.060
Herring gull	Mar-Dec	95,774	76,619	1.12	160.861
Black-headed gull	Apr-Oct	20	16	0.28	0.006
Great black-backed gull	Mar-Dec	19,472	15,578	1.68	49.068
Common tern	May-Sep	52,536	42,029	0.12	4.729
Caspian tern	May-Sep	22	18	0.61	0.010
Arctic tern	May-Sep	2,010	1,608	0.11	0.166
Black guillemot	Jan-Dec	9,524	6,667	0.40	6.477
Leach's storm-petrel	May-Oct	1,036	725	0.05	0.044
Northern gannet	Apr-Oct	84,248	58,974	3.20	267.333
Black-legged kittiwake	Apr-Oct	168,752	118,126	0.44	73.628
Common murre	May-Sep	89,320	62,524	0.99	87.685
Thick-billed murre	Apr-Oct	24	17	0.93	0.022
Razorbill	Apr-Oct	16,500	11,550	0.72	11.781
Atlantic puffin	Apr-Oct	48,348	33,844	0.46	22.054
TOTAL	Jan-Dec	651,141	539,790	-	859.176

Production

An energetic model developed for seabirds of the whole Gulf of St. Lawrence (4RST) (G. Chapdelaine, unpublished data) indicates that there are a total of 221,201 nestlings produced each year for all species combined (calculated by assuming that nestlings = number of breeding pairs \times 0.6). Multiplying the number of nestlings by the average mass for each species results in a total annual production of $0.001 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a P/B of 0.25 yr^{-1} . Bundy et al. (2001) estimated a P/B of 0.25 yr^{-1} for the Newfoundland-Labrador Shelf. When the minimum and maximum biomass values and the two previous P/B ratios were used, we obtained a production range of 0.0005 to $0.0011 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a production of $0.0010 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a P/B of 0.31 yr^{-1} .

Consumption

Estimated food Q/B for seabirds in the northern Gulf is 126.18 yr^{-1} (Chapdelaine, unpublished data). Based on the study of Barrett et al. (2006) for the North Atlantic, we estimated another Q/B of 122.38 yr^{-1} . When the minimum and maximum biomass values and the two previous P/B ratios were used, we obtained a consumption range of 0.257 to $0.507 \text{ t km}^{-2} \text{ yr}^{-1}$.

Based on the previous mean production ($0.0008 \text{ t km}^{-2} \text{ yr}^{-1}$) for seabirds and the minimum and maximum GE limits (0.1–1%), we obtained consumption values of 0.082 and $0.817 \text{ t km}^{-2} \text{ yr}^{-1}$. The resulting lower and upper consumption limits were 0.082 and $0.817 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean consumption of $0.450 \pm 0.520 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse model's solution was a consumption of $0.127 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a Q/B of 41.643 yr^{-1} .

Diet composition

Seabirds within the study area feed at a variety of trophic levels with most prey being small pelagic fish, benthic invertebrates, and pelagic crustaceans (Cairns et al. 1990). Great cormorants feed mostly on benthic fish, primarily flatfish and cunners (*Tautoglabrus adspersus*), while double-crested cormorants prey heavily on flatfish, sculpins (*Myoxocephalus* sp.), rock gunnells (*Pholis gunnellus*), and sand lance (*Ammodytes* spp.). The only data available from the Gulf of St. Lawrence for black guillemot showed that chicks are fed primarily with benthic fish, particularly sculpins, blennies, and tomcod (*Microgadus tomcod*) (Cairns 1981). Northern gannet, the largest breeding seabird species in the study area, preys on pelagic species such as mackerel but also on sand lance (Burton 1980). Herring gulls, which are the most abundant species in the study area, feed primarily on small pelagic fish and non-marine food (Threlfall 1968, Haycock and Threlfall 1975, Pierroti 1983), but quantitative dietary data from the Gulf are generally lacking for this species as well as for all other gulls, terns, storm-petrels, kittiwakes, and offshore alcids (Cairns et al. 1990). The diet of Arctic tern, recorded on Québec's North Shore (NAFO division 4S; Chapdelaine et al. 1985), as well as the diet of the common tern, the most abundant species in the eastern part of the area (NAFO division 4R), consist mainly of capelin, sand lance, and pelagic invertebrates. Black-legged kittiwakes are the most abundant species in the western part of the study area (NAFO division 4S) and feed primarily on copepods and euphausiids (Threlfall 1968, Maunder and Threlfall 1972). The final seabird diet was modified following Cairns et al. (1990) and Chapdelaine (unpublished data), who used all available information for the Gulf of St. Lawrence as well as extrapolated information from the closest ecosystems to create a complete diet for all seabird species found in the Gulf of St. Lawrence (north and south, NAFO divisions 4RST). There is no diet data available for Leach's storm-petrel, kittiwakes, murre, razorbills, or Atlantic puffins from the northern Gulf. Information for these species has been extrapolated from Labrador, eastern Newfoundland, and Nova Scotia (Bundy et al. 2000). Based on these different studies, we estimated the diet composition of seabirds used in modelling for the northern Gulf of St. Lawrence (Table 6).

Table 6. Diet composition (%) for seabirds used in modelling. Est: diet estimates from the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Prey	Seabirds				
	Mean	±SD	Min	Max	Est
Large cod					
Small cod	0.2	0.4	0.0	0.5	0.2
Large Green. halibut					
Small Green. halibut	0.4	0.6	0.0	0.8	0.4
American plaice	0.4	0.6	0.0	0.8	0.4
Flounders	0.4	0.6	0.0	0.8	0.4
Skates	0.4	0.6	0.0	0.8	0.4
Redfish					
Large demersals					
Small demersals	8.3	10.8	1.6	16.9	1.6
Capelin	43.7	34.3	21.9	76.0	43.7
Large pelagics	0.0	0.1	0.0	0.1	0.0
Pisci. small pelagics	9.7	15.1	0.2	21.5	0.9
Plank. small pelagics	30.1	37.3	5.8	61.6	38.9
Shrimp	0.6	1.0	0.0	1.4	1.3
Large crabs					
Small crabs					
Echinoderms					
Molluscs	0.0	0.1	0.0	0.1	0.0
Polychaetes					
Other bent. inver.	0.6	1.0	0.0	1.4	1.3
Large zooplankton	5.0	7.8	0.0	11.1	10.3
Small zooplankton	0.2	0.4	0.0	0.5	0.2
Phytoplankton					
Detritus					
Total	100.0		29.6	194.5	100.0
TRN	15				

Atlantic cod

Background

The northern Gulf cod stock overwinters in the deep waters off southwestern Newfoundland and then returns to the Gulf, moving northwards off Newfoundland's west coast (NAFO division 4R). Spawning takes place mainly during April and May in Esquiman Channel. During summer, the population migrates to the warmer coastal waters of Québec's lower North Shore and the west coast of Newfoundland.

Commercial landings increased considerably during the late 1950s and 1960s, but the stock declined to low levels by the mid to late 1970s. Following this decline, there was a period of recovery during the early 1980s before the stock collapsed in the early 1990s (Fréchet et al. 2005).

For the purpose of this study, Atlantic cod were divided into adults and juveniles, or more accurately, into large and small fish. Smaller fish prey mainly on invertebrates while larger fish feed mainly on fish. These changes tend to occur gradually with increasing length, but here we assume that the change occurs at 35 cm for cod (Lilly 1991). Northern Gulf cod of age 4+ generally represent fish ≥ 35 cm of length, at which size cod become more piscivorous and begin to recruit to the commercial fishery.

Catch

Landings for large cod (age 4+) in NAFO divisions 3Pn4RS are available for the 2003–2005 period (Fréchet et al. 2005). Since cod from these three zones are considered to be part of the same stock, landings from 3Pn were included in the model (4RS3Pn area: 109,406 km²). Also, catch from NAFO statistics (NAFO 2007) have been taken for area 3Pn4RS. Mean catch of large cod was $2.44 \times 10^{-2} \pm 1.67 \times 10^{-3}$ t km⁻² yr⁻¹. This value includes a by-catch value from the shrimp fishery of 2 t or 1.58×10^{-5} t km⁻² yr⁻¹ (L. Savard and J. Gauthier, Maurice-Lamontagne Institute, unpublished data). For the small cod group, a by-catch value from the shrimp fishery was estimated at $6.87 \times 10^{-5} \pm 3.77 \times 10^{-5}$ t km⁻² yr⁻¹ (L. Savard and J. Gauthier, Maurice-Lamontagne Institute, unpublished data). The inverse solution estimated catch values of 2.80×10^{-2} and 7.05×10^{-5} t km⁻² yr⁻¹, respectively, for large and small cod groups.

Biomass

The biomass of large cod was based on virtual population analysis estimates of cod biomass at the beginning of the year. The estimated average biomass of large cod was 49,119 t or 0.449 t km⁻² (SD = 0.073 t km⁻²; range: 0.366–0.500 t km⁻²) (Fréchet et al. 2005).

Assuming an annual instantaneous rate of natural mortality of 0.6 (since young fish are likely to have a higher natural mortality rate than older fish; M. Castonguay, pers. comm.) and a negligible catch of small cod, the numbers of 0-, 1-, and 2-year-old fish were estimated by back-calculation using an equation derived from Ricker (1980):

$$(8) N_{i-1} = N_i / e^{-z}$$

where N is abundance, i is year class, and Z is total mortality (here equal to natural mortality). Mean body mass was then multiplied by the abundance of each age class in order to obtain the biomass for the given group (this was not done for age 3 cod, for which biomass was directly taken from the VPA; Fréchet et al. 2005). Values of mean body mass were 0.010, 0.059, and 0.139 kg for fish of 0, 1, and 2 years of age, respectively (DFO, groundfish survey database, unpublished data). The biomass of age groups 0 to 3 were then summed in order to obtain a biomass estimate of small cod for each of the three years considered. This method yielded a mean annual biomass for small cod of 6,044 t or 0.055 t km^{-2} ($\text{SD} = 0.027 \text{ t km}^{-2}$; range: 0.030–0.083 t km^{-2}).

Production

P/B of large cod was estimated by a catch-curve analysis of groundfish survey data from NAFO divisions 4RS for the 2003–2005 period. The estimate of total mortality ($Z = 1.06 \text{ yr}^{-1}$) was determined from the slope of the regression line fitted to the downward side of the catch curve (Sinclair 2001). This instantaneous rate was then converted into real mortality rate ($A = 0.65 \text{ yr}^{-1}$; $A = 1 - e^{-Z}$, where Z is the instantaneous mortality rate according to Ricker 1980). Since we assume a steady state (no year-to-year change in biomass), total mortality A (0.65 yr^{-1}) is equal to the P/B ratio of cod in 2003–2005 (Allen 1971). The annual production estimate was $0.292 \pm 0.047 \text{ t km}^{-2} \text{ yr}^{-1}$. Production was also estimated by multiplying biomass by natural mortality (M), plus catch. Natural mortality for large cod was estimated at 0.20 yr^{-1} in 2003–2005 (DFO 2007). We obtained an annual production of $0.116 \pm 0.034 \text{ t km}^{-2} \text{ yr}^{-1}$. Combining the two methods resulted in a mean annual production of $0.204 \pm 0.125 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a production of $0.182 \text{ t km}^{-2} \text{ yr}^{-1}$, resulting in a P/B of 0.41 yr^{-1} .

For small cod, production was assumed to be equivalent to biomass multiplied by natural mortality (M), plus catch. Natural mortality for small cod was assumed to be 0.6 yr^{-1} . Based on previous biomass and catch values for small cod, we estimated a production range of 0.018 to $0.050 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to an annual production of $0.033 \pm 0.016 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a production of $0.050 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a P/B value of 0.90 yr^{-1} .

Consumption

A range of Q/B values was used to estimate the mean Q/B ratio for large cod. These values were based on different studies of food consumption by cod populations in the northwest Atlantic ($\text{Q/B} = 3.43 \text{ yr}^{-1}$; Pauly 1989, Froese and Pauly 2002) as well as in the Gulf of St. Lawrence ($\text{Q/B} = 1.96 \text{ yr}^{-1}$; Waiwood et al. 1980). The Q/B ratios for large cod varied between 1.96 and 3.43 yr^{-1} , corresponding to a consumption range between 0.718 and $1.716 \text{ t km}^{-2} \text{ yr}^{-1}$. Based on the previous mean production ($0.204 \text{ t km}^{-2} \text{ yr}^{-1}$) for large cod and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.679 and $2.036 \text{ t km}^{-2} \text{ yr}^{-1}$. The resulting lower and upper consumption limits were 0.679 and $2.036 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean consumption of $1.357 \pm 0.960 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a consumption of $1.121 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a Q/B of 2.496 yr^{-1} .

Two studies were used to estimate the Q/B ratio for small cod extrapolated from food intake measurements (daily or yearly consumption) and body mass or biomass of fish under study. This approach yielded Q/B ratios of 3.250 yr^{-1} (Waiwood et al. 1980) and 2.564 yr^{-1} (Grundwald and Koster 1994). This corresponded to a consumption range between 0.078 and $0.271 \text{ t km}^{-2} \text{ yr}^{-1}$. Based on the previous mean production ($0.033 \text{ t km}^{-2} \text{ yr}^{-1}$) for small cod and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.111 and $0.332 \text{ t km}^{-2} \text{ yr}^{-1}$. The resulting lower and upper consumption limits were 0.078 and $0.332 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean consumption of $0.205 \pm 0.180 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a consumption of $0.196 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a Q/B of 3.549 yr^{-1} .

Diet composition

Stomach content data were available for large and small cod groups from NAFO divisions 4RS from 2003 to 2005 (D. Chabot, unpublished data). The numbers of stomachs sampled for 2003, 2004, and 2005 were 652, 767, and 537 for large cod and 221, 311, and 307 for small cod, respectively. The fullness indices, including empty stomachs, were 0.89, 0.85, and 1.08 for 2003, 2004, and 2005 in large cod and 1.08, 0.90, and 1.07 in small cod. Overall, the most important prey items of large cod, in percent mass of stomach content, were shrimp, small crabs, large zooplankton, planktivorous small pelagics (mainly Atlantic herring), small American plaice, and capelin (81.7% of the diet; Table 7). The most important prey items of small cod were shrimp, large zooplankton, capelin, and small demersals (93.7% of the diet; Table 7).

Table 7. Diet compositions (%) for large and small cod used in modelling. Est: diet estimates from the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Prey	Large cod (> 35 cm)					Small cod (≤ 35 cm)				
	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	1.3	2.1	0.0	3.7	0.3	0.0	0.0	0.0	0.0	0.0
Large Green. halibut										
Small Green. halibut	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
American plaice	8.5	5.9	0.0	15.3	0.9	0.0	0.0	0.0	0.0	0.0
Flounders	0.2	0.2	0.0	0.3	0.2	0.0	0.0	0.0	0.0	0.0
Skates	0.1	0.2	0.0	0.3	0.1					
Redfish	4.7	5.6	0.0	17.2	9.0	0.3	0.5	0.0	0.9	0.3
Large demersals										
Small demersals	6.6	4.9	0.0	13.8	0.1	7.8	4.0	4.1	12.0	5.2
Capelin	8.3	4.8	0.0	12.2	11.9	10.3	4.5	5.0	13.3	12.6
Large pelagics										
Pisci. small pelagics	2.0	1.4	0.0	3.5	0.2	0.0	0.0	0.0	0.0	0.0
Plank. small pelagics	14.1	3.7	0.0	20.3	14.2	1.3	0.8	0.5	2.1	2.0
Shrimp	19.1	4.0	8.9	86.2	30.0	38.8	8.8	24.8	51.0	32.6
Large crabs	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Small crabs	16.6	8.3	0.0	25.0	5.0	1.7	1.3	0.3	2.9	0.6
Echinoderms	1.7	1.0	0.0	2.5	2.3	0.0	0.0	0.0	0.0	0.0
Molluscs	0.9	0.4	0.0	1.4	0.9	0.1	0.1	0.0	0.2	0.1
Polychaetes	0.8	0.3	0.1	1.1	0.8	2.3	1.1	1.0	3.1	3.0
Other bent. inver.	0.2	0.2	0.0	0.5	0.2	0.3	0.3	0.0	0.7	0.3
Large zooplankton	15.1	10.3	8.2	53.7	24.0	36.9	15.4	25.1	54.3	43.1
Small zooplankton	0.0	0.0	0.0	0.1	0.0	0.3	0.3	0.1	0.6	0.3
Phytoplankton										
Detritus										
Total	100.0		17.3	257.1	100.0	100.0		61.0	141.2	100.0
TRN	19					18				

Greenland halibut

Background

Greenland halibut (*Reinhardtius hippoglossoides*) is a deep-water flatfish present in the North Atlantic and North Pacific. In the northwest Atlantic, it is found from Arctic regions to Georges Bank (Bowering 1983). The Gulf of St. Lawrence population is considered to be a small stock, isolated from the main northwest Atlantic stock, completing its entire life cycle within the Gulf (DFO 2006a).

Directed fishing for this species with bottom trawls and gillnets developed after the mid-1970s. Landings increased in the 1980s to reach an all-time high in 1987 (11,000 t) but declined at the beginning of the 1990s and are now around 3,000–4,000 t (DFO 2006a).

Greenland halibut were divided into large and small fish. Although there is an apparent change in diet composition when fish reach lengths of about 20 cm (Bundy et al. 2000), we separated Greenland halibut into fish larger or smaller than 40 cm, the size at which they are first recruited to the fishery (Brodie 1991). Greenland halibut greater than 40 cm in length are equivalent to fish aged six years and older (Brodie 1991).

Catch

According to the NAFO fisheries statistics (NAFO 2007) and the advisory report (DFO 2006a), the mean annual landing of large Greenland halibut during the 2003–2005 period was $3.67 \times 10^{-2} \pm 2.03 \times 10^{-3} \text{ t km}^{-2} \text{ yr}^{-1}$. This value includes by-catch from the shrimp fishery of 4 t or $3.83 \times 10^{-5} \text{ t km}^{-2} \text{ yr}^{-1}$ (L. Savard and J. Gauthier, Maurice-Lamontagne Institute, unpublished data). For the small Greenland halibut group, a by-catch value from the shrimp fishery was estimated at $6.95 \times 10^{-4} \pm 1.14 \times 10^{-4} \text{ t km}^{-2} \text{ yr}^{-1}$ (L. Savard and J. Gauthier, Maurice-Lamontagne Institute, unpublished data). The inverse solution estimated catch values of 3.65×10^{-2} and $6.97 \times 10^{-4} \text{ t km}^{-2} \text{ yr}^{-1}$, respectively, for large and small Greenland halibut groups.

Biomass

Annual biomass estimates were obtained from groundfish survey data for the 2003–2005 period. Length-frequency data from each year were extrapolated to the whole northern Gulf area using the PACES software to obtain an estimate of halibut abundance for this zone. Total biomass was estimated each year by multiplying the abundance estimate for each length increment by mean mass-at-length (derived from length–mass relationships) and summing the results. This resulted in mean biomass estimates for the 2003–2005 period of 62,014 t or 0.597 t km^{-2} (SD = 0.052 t km^{-2} ; range = $0.561\text{--}0.634 \text{ t km}^{-2}$) and 181,583 t or 1.749 t km^{-2} (SD = 0.974 t km^{-2} ; range = $1.060\text{--}2.438 \text{ t km}^{-2}$) for large and small Greenland halibut, respectively.

Production

Due to the lack of reliable information on production (P) and total mortality (Z) for this species, it was assumed that production was equivalent to biomass multiplied by natural mortality (M), plus catch. Natural mortality for large Greenland halibut ($M = 0.17 \text{ yr}^{-1}$) was estimated using FishBase (Froese and Pauly 2002) and a maximal length of 96.5 cm along with a water temperature of 3°C . When the biomass and catch values were used, we obtained a production range of 0.134 to $0.142 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean production of $0.138 \pm 0.006 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a production of $0.136 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a P/B of 0.23 yr^{-1} .

For small Greenland halibut, it was assumed that natural mortality was higher (younger fish generally have a higher M than older fish), so a textbook range of 0.4 to 0.6 yr^{-1} was assigned to this group. When the biomass and catch values were used, we obtained a production range of 0.425 to $1.464 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean production of $0.875 \pm 0.453 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a production of $0.525 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a P/B of 0.30 yr^{-1} .

Consumption

A Q/B ratio (1.660 yr^{-1}) was estimated using daily food requirements for 6- to 20-year-old Greenland halibut from the northwest Atlantic (Chumakov and Podrazhanskaya 1986). Another Q/B ratio (2.300 yr^{-1}) was calculated using FishBase (Froese and Pauly 2002) for fish having a mean mass of 752.97 g and a mean length of 43.94 cm (mean characteristics of the large Greenland halibut group) at 3°C (DFO, groundfish survey database, unpublished data). Finally, we estimated a Q/B of 1.082 yr^{-1} from the study of Laurinolli et al. (2004) in the Scotian Shelf and Bay of Fundy. When the minimum and maximum biomass values and the three previous Q/B ratios were used, we obtained a total consumption of $1.004 \text{ t km}^{-2} \text{ yr}^{-1}$ (range: $0.607\text{--}1.459 \text{ t km}^{-2} \text{ yr}^{-1}$) for large Greenland halibut. Based on the previous mean production ($0.138 \text{ t km}^{-2} \text{ yr}^{-1}$) for large Greenland halibut and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.460 and $1.379 \text{ t km}^{-2} \text{ yr}^{-1}$. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used $0.597 \text{ t km}^{-2} \text{ yr}^{-1}$ instead of $0.460 \text{ t km}^{-2} \text{ yr}^{-1}$. The resulting lower and upper consumption limits were thus 0.597 and $1.459 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean consumption of $1.028 \pm 0.609 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a consumption of $0.605 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a Q/B of 1.013 yr^{-1} .

Q/B values for small Greenland halibut were obtained from four different sources. Using the mean daily consumption of 5-year-old Greenland halibut ($< 40 \text{ cm}$) (Chumakov and Podrazhanskaya 1986), the Q/B ratio was 4.427 yr^{-1} . The estimate obtained from FishBase (Froese and Pauly 2002), for fish having a mean mass of 159.49 g and a mean length of 27.18 cm (mean characteristics of the small Greenland halibut group) at 3°C (DFO, groundfish survey database, unpublished data), was slightly lower, with a Q/B value of 3.200 yr^{-1} . A third estimate (Q/B: 2.665 yr^{-1}) was obtained from a feeding study conducted in West Greenland (Pedersen and Riget 1992a). Finally, we estimated a Q/B of 5.048 yr^{-1} from the study of Laurinolli et al. (2004) in the Scotian Shelf and Bay of Fundy. When the minimum and maximum biomass values and the previous Q/B ratios were used, we obtained a total consumption of $6.708 \text{ t km}^{-2} \text{ yr}^{-1}$ (range: $2.825\text{--}12.308 \text{ t km}^{-2} \text{ yr}^{-1}$) for small Greenland halibut. Based on the previous minimum and

maximum production values ($0.425\text{--}1.464 \text{ t km}^{-2} \text{ yr}^{-1}$) for small Greenland halibut and the minimum and maximum GE limits (10–30%), we obtained consumption values of 1.416 and $14.637 \text{ t km}^{-2} \text{ yr}^{-1}$. We used here the minimum and maximum production values instead of the mean production to increase the range of potential consumption based on initial inverse modelling runs. Also, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used $1.749 \text{ t km}^{-2} \text{ yr}^{-1}$ instead of $1.416 \text{ t km}^{-2} \text{ yr}^{-1}$. The resulting lower and upper consumption limits were thus 1.749 and $14.637 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean consumption of $8.193 \pm 9.113 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a consumption of $1.762 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a Q/B of 1.007 yr^{-1} .

Diet composition

Stomach content data for Greenland halibut from NAFO divisions 4RS were available from 2003 to 2004 (D. Chabot, unpublished data). Sample sizes for 2003 and 2004 were 558 and 202 for large Greenland halibut and 1138 and 498 for small Greenland halibut, respectively. The stomach fullness indices, including empty stomachs, were 0.48 for both 2003 and 2004 in large Greenland halibut. Similarly, it was 0.69 for both years in small Greenland halibut. Overall, the most important prey items of large Greenland halibut, in percent mass of stomach content, were shrimp, small demersals, capelin, and large zooplankton (91.8% of the diet; Table 8). The most important prey items of small Greenland halibut were shrimp, large zooplankton, and capelin, (96.8% of the diet; Table 8).

Table 8. Diet compositions (%) for large and small Greenland halibut used in modelling. Est: diet estimates from the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Prey	Large Greenland halibut (> 40 cm)					Small Greenland halibut (≤ 40 cm)				
	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Large Green. halibut										
Small Green. halibut	2.4	3.4	0.0	4.8	4.4	0.1	0.1	0.0	0.1	0.1
American plaice	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.1	0.1
Flounders	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.1	0.1
Skates	0.1	0.1	0.0	0.2	0.1					
Redfish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Large demersals										
Small demersals	28.3	4.3	25.2	31.3	25.2	2.9	1.0	2.2	3.6	2.2
Capelin	11.8	1.2	10.9	12.6	11.2	28.2	0.5	27.9	28.6	28.2
Large pelagics	0.0	0.0	0.0	0.0	0.0					
Pisci. small pelagics	1.7	2.4	0.0	3.4	0.0	0.0	0.0	0.0	0.0	0.0
Plank. small pelagics	3.7	5.2	0.0	7.4	5.4	0.1	0.1	0.0	0.1	0.1
Shrimp	45.1	15.5	34.2	56.1	46.7	34.4	10.4	27.0	41.7	34.8
Large crabs	0.0	0.0	0.0	0.0	0.0					
Small crabs	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Echinoderms	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Molluscs	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polychaetes	0.3	0.4	0.0	0.6	0.3	0.0	0.0	0.0	0.0	0.0
Other bent. inver.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Large zooplankton	6.6	0.5	6.3	7.0	6.6	34.2	0.7	33.7	34.7	34.5
Small zooplankton	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Phytoplankton										
Detritus										
Total	100.0		76.6	123.4	100.0	100.0		90.8	109.2	100.0
TRN	20					17				

American plaice, flounders, and skates

Background

All flatfish other than Greenland halibut were divided into three groups: American plaice (*Hippoglossoides platessoides*), flounders, and skates.

American plaice is widely distributed throughout the northwest Atlantic (from west Greenland to the Gulf of Maine) and is usually found at intermediate depths (80–250 m) (Morin et al. 1998). It has been exploited in NAFO divisions 4RS since 1947, with commercial catches peaking in 1977. Annual catches then began to fall until the mid-1980s, when they levelled off at around 2,000 t. However, yearly landings have since declined to around 100 t in the recent years.

The flounder group consists of witch flounder (*Glyptocephalus cynoglossus*), yellowtail flounder (*Limanda ferruginea*), fourspot flounder (*Paralichthys oblongus*), and winter flounder (*Pseudopleuronectes americanus*). Flounders were grouped together on the basis of their similar feeding behaviour. These four species are sedentary bottom-dwelling flatfish that live in relatively deep water, except for winter flounder, which lives mostly in infra-littoral waters. Their distribution ranges from the coast of Labrador to North Carolina. Since the 1950s, important commercial catches have occurred in the deep waters bordering the Laurentian Channel. A long-standing fishery has also been in place in shallower waters for winter flounder. The key species of the flounder group is witch flounder, mainly because of its high biomass (95% of total flounder biomass) and commercial significance.

The skate group included mainly two species: the thorny skate (*Amblyraja radiata*), considered here as the key species for the group (78.9% of total skate biomass) and the smooth skate (*Malacoraja senta*; 20.8% of total skate biomass); another species, the winter skate (*Leucoraja ocellata*), represented only 0.3% of total skate biomass. The thorny skate is widely distributed throughout the North Atlantic. The greatest concentrations are generally found in the higher part of continental shelves, at depths greater than 110 m (McEachran et al. 1976). The smooth skate is found throughout the northwest Atlantic, from the Gulf of St. Lawrence to Georges Bank (Scott and Scott 1988). Surveys conducted since the 1940s have shown that the greatest concentrations are found in the Gulf of St. Lawrence, on the Grand Banks, and on the Scotian Shelf. This species lives at depths of 50 to 700 m but is mostly caught between 90 and 325 m (McKone and LeGrow 1983). Fishing activity is less important for the smooth skate than for the thorny skate.

Catch

According to the landing statistics (NAFO 2007), mean annual landings during the 2003–2005 period in NAFO divisions 4RS were 151 t or $1.46 \times 10^{-3} \pm 2.35 \times 10^{-4} \text{ t km}^{-2} \text{ yr}^{-1}$ for American plaice, 423 t or $4.08 \times 10^{-3} \pm 9.52 \times 10^{-4} \text{ t km}^{-2} \text{ yr}^{-1}$ for flounders, and 37 t or $3.53 \times 10^{-4} \pm 2.21 \times 10^{-4} \text{ t km}^{-2} \text{ yr}^{-1}$ for skates. These landings include by-catch values from the shrimp fishery of 2.63×10^{-4} and 2.97×10^{-4} , respectively, for American plaice and flounders (L. Savard and J. Gauthier, Maurice-Lamontagne Institute, unpublished data). The inverse solution estimated catch values of 1.43×10^{-3} , 4.21×10^{-3} , and $3.84 \times 10^{-4} \text{ t km}^{-2} \text{ yr}^{-1}$ for American plaice, flounders, and skates, respectively.

Biomass

Annual biomass estimates for the three groups were obtained using *PACES* to analyze research survey data from NAFO divisions 4RS during the 2003–2005 period. Mean biomass in NAFO divisions 4RS was estimated at 38,921 t or 0.375 t km^{-2} ($\text{SD} = 0.114 \text{ t km}^{-2}$; range: $0.294\text{--}0.456 \text{ t km}^{-2}$) for American plaice, 6,893 t or 0.066 t km^{-2} ($\text{SD} = 0.032 \text{ t km}^{-2}$; range: $0.044\text{--}0.089 \text{ t km}^{-2}$) for flounders, and 8,158 t or 0.079 t km^{-2} ($\text{SD} = 0.021 \text{ t km}^{-2}$; range: $0.063\text{--}0.094 \text{ t km}^{-2}$) for skates.

Production

There was no information available on production or total mortality (Z) of American plaice, flounders, or skates within the study area. However, Morin et al. (2001) estimated a Z of 0.46 (and then $A = P/B = 0.37 \text{ yr}^{-1}$ according to Ricker [1980]) for American plaice from 1998 to 2000 in the southern Gulf. When the minimum and maximum biomass values were used, we obtained production ranges of 0.108 to $0.168 \text{ t km}^{-2} \text{ yr}^{-1}$. Production was also estimated by multiplying biomass by natural mortality (M), plus catch. Natural mortality was assumed to be 0.220 yr^{-1} for American plaice (Pitt 1982). We obtained production ranges of 0.066 to $0.102 \text{ t km}^{-2} \text{ yr}^{-1}$ when the minimum and maximum biomass values were used. Combining the two methods resulted in a mean annual production of $0.111 \pm 0.042 \text{ t km}^{-2} \text{ yr}^{-1}$ (range: $0.066\text{--}0.168 \text{ t km}^{-2} \text{ yr}^{-1}$). The inverse solution estimated a production for American plaice of $0.132 \text{ t km}^{-2} \text{ yr}^{-1}$, resulting in a P/B of 0.35 yr^{-1} .

For flounders and skates, production was estimated by multiplying biomass by natural mortality (M), plus catch. Natural mortality was assumed to be 0.214 yr^{-1} for skates (Simon and Frank 1995). Due to a lack of information, natural mortality of flounders was assumed to be 0.200 yr^{-1} . When the minimum and maximum biomass values were used for each group, we obtained production ranges of 0.018 to $0.030 \text{ t km}^{-2} \text{ yr}^{-1}$ for flounders and 0.014 to $0.021 \text{ t km}^{-2} \text{ yr}^{-1}$ for skates. Production values estimated by the inverse solution were $0.028 \text{ t km}^{-2} \text{ yr}^{-1}$ ($P/B = 0.42 \text{ yr}^{-1}$) for flounders and $0.020 \text{ t km}^{-2} \text{ yr}^{-1}$ ($P/B = 0.25 \text{ yr}^{-1}$) for skates.

Consumption

For American plaice, FishBase provided an initial Q/B estimate (Froese and Pauly 2002). The Q/B value obtained in this way was 3.5 yr^{-1} for American plaice having a mean mass of 110.16 g and a mean length of 24.8 cm (mean characteristics; DFO, groundfish survey database, unpublished data) at 3°C . A second estimate of consumption was derived from daily ration data using the model of Elliott and Persson (1978) with fish from the Grand Banks of Newfoundland (Zamarro 1992). Daily consumption values were 0.04% to 0.64% of body mass per day, with a final mean of 0.34% . Accordingly, the mean annual Q/B ratio was 1.241 yr^{-1} . A third study, with fish from Passamaquoddy Bay (New Brunswick), was used to determine consumption for American plaice (MacDonald and Waiwood 1987). The authors estimated food consumption to

be 1.28% of body mass per day, resulting in a Q/B ratio of 4.672 yr^{-1} (assuming that feeding is constant throughout the year). When the minimum and maximum biomass values and the three previous Q/B ratios were used, we obtained a total consumption of $1.176 \text{ t km}^{-2} \text{ yr}^{-1}$ (range: $0.365\text{--}2.129 \text{ t km}^{-2} \text{ yr}^{-1}$) for American plaice. Based on the previous mean production ($0.111 \text{ t km}^{-2} \text{ yr}^{-1}$) for American plaice and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.371 and $1.112 \text{ t km}^{-2} \text{ yr}^{-1}$. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used $0.375 \text{ t km}^{-2} \text{ yr}^{-1}$ instead of $0.365 \text{ t km}^{-2} \text{ yr}^{-1}$. The resulting lower and upper consumption limits were thus 0.375 and $2.129 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean consumption of $1.252 \pm 1.240 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a consumption of $0.533 \text{ t km}^{-2} \text{ yr}^{-1}$ for American plaice, representing a Q/B of 1.421 yr^{-1} .

Consumption estimates for the flounder group were derived from different sources (Table 9).

Table 9. Q/B ratios (yr^{-1}) for flounders in different regions of the northwest Atlantic. When Q/B ratios were estimated using FishBase (Froese and Pauly 2002), mean length and mass observed during the DFO survey (unpublished data) and a temperature of 3°C were used.

Species	Q/B	Reference
Witch flounder	3.600	FishBase: 96.88 g and 26.00 cm
	2.599	Bundy et al. (2000)
	2.400	Bundy (2004)
	3.255	Laurinolli et al. (2004)
	2.964	Mean
Yellowtail flounder	4.600	Grosslein et al. (1980)
	2.639	Bundy et al. (2000)
	3.200	FishBase: 159.52 g and 26.26 cm
	4.700	Bundy (2004)
	2.574	Laurinolli et al. (2004)
Winter flounder	3.543	Mean
	2.500	FishBase: 528.69 g and 34.48 cm
	1.700	Bundy (2004)
	3.445	Laurinolli et al. (2004)
	2.548	Mean

When the annual biomass values for each flounder species were used and individual consumption values summed, this resulted in a total consumption range of 0.130 to $0.266 \text{ t km}^{-2} \text{ yr}^{-1}$. Based on the previous mean production ($0.024 \text{ t km}^{-2} \text{ yr}^{-1}$) for flounders and the minimum and maximum GE limits (10–30%), we obtained two other consumption values of 0.080 and $0.240 \text{ t km}^{-2} \text{ yr}^{-1}$, respectively. The resulting lower and upper consumption limits were thus 0.080 and $0.266 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean consumption of $0.173 \pm 0.131 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a consumption of $0.143 \text{ t km}^{-2} \text{ yr}^{-1}$ for flounders, representing a Q/B of 2.151 yr^{-1} .

For skates, consumption estimates were also derived from different sources (Table 10).

Table 10. Q/B ratios (yr^{-1}) for skates in different regions of the northwest Atlantic. When Q/B ratios were estimated using FishBase (Froese and Pauly 2002), mean length and mass observed during the DFO survey (unpublished data) and a temperature of 3°C were used.

Species	Q/B	Reference
Thorny skate	3.400	FishBase: 127.52 g and 23.67 cm
	2.369	Dolgov (1997) ^a
	2.865	Vinter (1989)
	1.880	Bundy (2004)
	4.215	Laurinolli et al. (2004)
	2.946	Mean
Smooth skate	6.621	Laurinolli et al. (2004)
	4.200	FishBase: 45.12 g and 21.30 cm
	5.410	Mean
Winter skate	1.755	Laurinolli et al. (2004)
	3.100	FishBase: 203.45 g and 28.98 cm
	2.428	Mean

^a: Estimated annual consumption from the Barents Sea (Dolgov 1997) was divided by mean biomass, resulting in an annual Q/B ratio of 2.369 yr^{-1} for our study area.

When the annual biomass values for each skate species were used and individual consumption values summed, this resulted in a total consumption range of 0.200 to $0.344 \text{ t km}^{-2} \text{ yr}^{-1}$. Based on the previous mean production ($0.017 \text{ t km}^{-2} \text{ yr}^{-1}$) for skates and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.057 and $0.172 \text{ t km}^{-2} \text{ yr}^{-1}$. However, assuming that this species would eat at least as much food as its biomass ($\text{Q/B} \geq 1$), we used $0.079 \text{ t km}^{-2} \text{ yr}^{-1}$ instead of $0.057 \text{ t km}^{-2} \text{ yr}^{-1}$. The resulting lower and upper consumption limits were thus 0.079 and $0.344 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean consumption of $0.211 \pm 0.187 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a consumption of $0.102 \text{ t km}^{-2} \text{ yr}^{-1}$ for skates, representing a Q/B of 1.294 yr^{-1} .

Diet composition

Diet data from NAFO divisions 4RS during the 2003–2005 period were unavailable for all three groups, so studies from other areas and time periods were used instead. For American plaice, we used the diet compositions found by Bundy (2004) for the eastern Scotian Shelf (1999–2000; $n = 727$), by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s), and by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997) to construct the upper and lower limits used to constrain values in inverse modelling (Table 11). The most important prey items of American plaice were large zooplankton, planktivorous small pelagics, other benthic invertebrates, polychaetes, and capelin (78.5% of the diet; Table 11).

For flounders, very little diet information was available. Stomach content data for witch flounder from NAFO divisions 4RS were available from 2003 to 2005 ($n = 20$; D. Chabot, unpublished data). The summer diet of witch flounder on Flemish Cap was also used and is principally made up of polychaetes (80.2% by volume), other benthic invertebrates (8.4% by volume), echinoderms (5.7% by volume), and bivalves (4.6% by volume) (Rodriguez-Marin et al. 1994). Due to the uncertainties with diet data, we also used the diet compositions found by Bundy (2004) for the eastern Scotian Shelf (1999–2000; $n = 1313$), by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s), and by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997). The most important prey items in the resulting diet of flounders were polychaetes, other benthic invertebrates, and large zooplankton (84.2% of the diet; Table 11).

For skates, we used the diet compositions found by Bundy (2004) for the eastern Scotian Shelf (1999–2000; $n = 404$), by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s), and by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997). The most important prey items in the resulting diet of skates were small planktivorous pelagics, large zooplankton, small crabs, small demersals, and polychaetes (76.6% of the diet; Table 11).

Table 11. Diet compositions (%) for American plaice, flounders, and skates used in modelling. Est: diet estimates from the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Prey	American plaice					Flounders				
	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	0.0	0.0	0.0	0.0	0.0					
Large Green. halibut										
Small Green. halibut	0.0	0.0	0.0	0.0	0.0					
American plaice	0.1	0.0	0.0	0.1	0.1					
Flounders	0.1	0.1	0.0	0.1	0.1					
Skates										
Redfish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Large demersals										
Small demersals	1.0	1.6	0.0	2.9	0.1	0.4	0.5	0.0	7.1	0.4
Capelin	9.8	12.3	0.0	24.0	10.7	0.1	0.1	0.0	3.9	0.1
Large pelagics										
Pisci. small pelagics	0.0	0.1	0.0	0.1	0.0					
Plank. small pelagics	13.8	20.4	0.0	18.0	2.8	1.3	2.2	0.0	5.2	1.6
Shrimp	7.4	9.6	0.0	18.8	3.4	1.5	1.2	0.0	2.8	1.2
Large crabs						0.0	0.0	0.0	0.0	0.0
Small crabs	1.7	1.9	0.0	3.9	0.1	0.4	0.6	0.0	2.2	0.1
Echinoderms	7.3	4.3	0.0	30.9	12.2	6.4	10.8	0.0	38.4	6.8
Molluscs	3.8	2.5	0.0	51.4	19.0	5.0	7.8	0.0	40.6	18.8
Polychaetes	11.3	7.9	0.0	21.0	13.4	46.8	25.1	8.2	80.1	33.3
Other bent. inver.	12.3	1.6	0.0	38.5	20.2	14.0	12.0	0.0	63.7	20.2
Large zooplankton	31.3	25.3	8.4	99.1	17.8	23.4	34.1	0.0	76.4	16.0
Small zooplankton	0.1	0.1	0.0	1.1	0.1	0.0	0.0	0.0	0.1	0.0
Phytoplankton										
Detritus						0.6	1.3	0.0	4.1	1.4
Total	100.0		8.4	309.8	100.0	100.0		8.2	324.8	100.0
TRN	17					14				

Table 11. Cont.

Prey	Skates				
	Mean	± SD	Min	Max	Est
Large cod					
Small cod	1.1	2.0	0.0	3.4	0.1
Large Green. halibut					
Small Green. halibut	0.0	0.0	0.0	0.1	0.0
American plaice	0.1	0.1	0.0	0.2	0.1
Flounders	0.2	0.3	0.0	0.5	0.2
Skates	0.0	0.0	0.0	0.0	0.0
Redfish	4.6	7.8	0.0	13.6	11.0
Large demersals					
Small demersals	9.3	8.8	0.5	35.5	2.0
Capelin	4.5	7.0	0.0	12.6	8.9
Large pelagics					
Pisci. small pelagics	2.2	3.6	0.0	6.4	0.5
Plank. small pelagics	29.3	30.8	0.0	81.4	15.3
Shrimp	5.4	3.7	1.4	8.6	2.9
Large crabs					
Small crabs	13.1	8.1	4.4	41.9	4.8
Echinoderms	0.2	0.2	0.0	0.3	0.2
Molluscs	0.3	0.4	0.0	0.8	0.3
Polychaetes	8.4	4.9	3.5	14.1	7.8
Other bent. inver.	4.8	5.3	0.0	10.8	8.5
Large zooplankton	16.5	28.4	0.0	49.3	37.3
Small zooplankton	0.0	0.1	0.0	0.1	0.0
Phytoplankton					
Detritus					
Total	100.0		9.7	279.6	100.0
TRN	18				

Redfish and demersal feeders

Background

The demersal feeders represent deep-water demersal species from NAFO divisions 4RS. Because of its economic and ecological importance in the system, redfish was treated separately while the remaining demersal species were divided into large and small demersal feeders.

Redfish distribution in the northwest Atlantic ranges from west Greenland to the Gulf of Maine (Atkinson and Melteff 1987). Two redfish species are known to be the main component of the northwest Atlantic stock: *Sebastes mentella*, which generally occupies waters deeper than 250 m, and *S. fasciatus*, usually found in shallower waters down to 300 m. Redfish usually inhabit waters from 100 to 700 m in depth and are ovoviviparous. Mating usually occurs in September or October, and females release live young from April to July. Redfish grow quite slowly, generally taking 8 to 10 years before being recruited to the commercial fishery at approximately 25 cm in length. These species have been commercially fished since the early 1950s, but a moratorium was imposed on redfish fishing in 1995 in the Gulf of St. Lawrence (Gascon 2003).

The large demersal feeders are mainly made up of white hake (*Urophycis tenuis*), black dogfish (*Centroscyllium fabricii*), marlin spike (*Nezumia bairdi*), Atlantic halibut (*Hippoglossus hippoglossus*), wolffish (*Anarhichas* spp.), common lumpfish (*Cyclopterus lumpus*), haddock (*Melanogrammus aeglefinus*), longfin hake (*Urophycis chesteri*), large eelpout (Zoarcidae), monkfish (*Lophius americanus*), and grenadiers (Macrouridae). Information was very limited for most of these species in NAFO divisions 4RS.

The small demersal feeders include sculpins (Cottidae), small eelpouts (Zoarcidae), fourbeard rockling (*Enchelyopus cimbrius*), Atlantic hagfish (*Myxine glutinosa*), cunners (*Tautoglabrus adspersus*), gunnels (Pholidae), lumpsuckers (*Eumicrotremus* spp.), snailfish (Liparidae), and blennies (Stichaeidae). Juvenile large demersals were also considered as small demersal feeders. Unfortunately, little is known about these species and only scant information from the study area was available.

Catch

Total landings for redfish and the large demersal feeder group in NAFO divisions 4RS during the 2003–2005 period were calculated by summing the NAFO landing statistics for each of the species listed above (NAFO 2007). Since there is no fishery for species in the small demersal feeder group and by-catch information was unavailable, catch was set at zero for this group. For redfish, the average annual landings were 535 t or $5.15 \times 10^{-3} \text{ t km}^{-2} \text{ yr}^{-1}$ ($\text{SD} = 5.57 \times 10^{-4} \text{ t km}^{-2} \text{ yr}^{-1}$). These landings include by-catch values from the shrimp fishery of 2.94×10^{-4} (L. Savard and J. Gauthier, Maurice-Lamontagne Institute, unpublished data). For the large demersal feeders, Atlantic halibut (59% of total landings), lumpfish (32%), and white hake (3%) were the main species caught in 4RS during the 2003–2005 period. The average annual catch of the large demersal feeders was estimated at 424 t or $4.08 \times 10^{-3} \text{ t km}^{-2} \text{ yr}^{-1}$ ($\text{SD} = 5.68 \times 10^{-4} \text{ t km}^{-2} \text{ yr}^{-1}$). The inverse solution estimated catch values of 5.25×10^{-3} and $3.95 \times 10^{-3} \text{ t km}^{-2} \text{ yr}^{-1}$ for redfish and large demersal feeders, respectively.

Biomass

The scientific survey provided data from NAFO divisions 4RS during the 2003–2005 period to estimate annual biomass. For redfish, length-frequency data from each year were extrapolated to the whole northern Gulf area using the *PACES* software. Total biomass was estimated each year by multiplying the abundance estimate for each length increment by the mean mass-at-length (derived from length–mass relationships) and summing the results. For the large demersal feeder group, total biomass in the study area for each species was directly computed with *PACES* and results were summed. Average annual biomass estimates were 500,921 t or 4.825 t km^{-2} ($\text{SD} = 0.776 \text{ t km}^{-2}$; range: $4.276\text{--}5.374 \text{ t km}^{-2}$) for redfish and 20,871 t or 0.201 t km^{-2} ($\text{SD} = 0.148 \text{ t km}^{-2}$; range: $0.096\text{--}0.306 \text{ t km}^{-2}$) for large demersal feeders.

Biomass for the small demersal feeder group was determined in the same way as for their large counterparts. Average annual biomass was estimated at 15,452 t or 0.149 t km^{-2} ($\text{SD} = 0.048 \text{ t km}^{-2}$) corresponding to a range of 0.115 to 0.183 t km^{-2} for the entire study area during the 2003–2005 period. However, based on initial inverse modelling runs (see the following production section) and due to the large uncertainty related to the biomass of this group, the previous values seemed too low to meet predator demands. Hence these values were increased for small demersals ($0.260 \pm 0.205 \text{ t km}^{-2}$; range: $0.115\text{--}0.405 \text{ t km}^{-2}$).

Production

Information on production and total mortality (Z) of redfish and large demersal species was lacking. Production was therefore assumed to be equivalent to biomass multiplied by natural mortality (M), plus the catch (Allen 1971). Natural mortality (M) was assumed to range between 0.125 yr^{-1} (Bundy et al. 2000) and 0.232 yr^{-1} for redfish (Bundy 2004), and to be 0.200 yr^{-1} for large demersal feeders (Hurlbut and Poirier 2001). When the minimum and maximum biomass values were used for each group, we obtained production ranges of 0.540 to $1.251 \text{ t km}^{-2} \text{ yr}^{-1}$ for redfish and 0.023 to $0.065 \text{ t km}^{-2} \text{ yr}^{-1}$ for large demersal feeders. Production values estimated by the inverse solution were $0.540 \text{ t km}^{-2} \text{ yr}^{-1}$ ($P/B = 0.11 \text{ yr}^{-1}$) for redfish and $0.057 \text{ t km}^{-2} \text{ yr}^{-1}$ ($P/B = 0.28 \text{ yr}^{-1}$) for large demersal feeders.

Due to the large uncertainty related to the data of the small demersal feeders, we used the mean P/B value (0.42 yr^{-1}) obtained for the mid-1980 (0.46 yr^{-1}) and mid-1990 (0.38 yr^{-1}) models. When the initial minimum and maximum biomass values were used, we obtained a production range of 0.048 to $0.077 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean production value of $0.063 \pm 0.020 \text{ t km}^{-2} \text{ yr}^{-1}$. However, based on initial inverse modelling runs, the previous values seemed to be too low to meet predator demands. A production of $0.292 \text{ t km}^{-2} \text{ yr}^{-1}$ was required and was thus used as the maximum production limit. The resulting lower and upper production limits were thus 0.048 to $0.292 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean of $0.170 \pm 0.173 \text{ t km}^{-2} \text{ yr}^{-1}$. This mean production value was related to a biomass value of 0.405 t km^{-2} (see the previous biomass section). The production value estimated by the inverse solution was $0.289 \text{ t km}^{-2} \text{ yr}^{-1}$ ($P/B = 1.11 \text{ yr}^{-1}$) for small demersal feeders.

Consumption

FishBase was used to estimate the Q/B ratio of redfish assuming a water temperature of 3°C (Froese and Pauly 2002). This resulted in Q/B ratios of 3.3 yr⁻¹ for fish having a mean mass of 139.35 g and a mean length of 21.53 cm (mean characteristics; DFO, groundfish survey database, unpublished data). Other information on redfish consumption is available. Dolgov and Revetnyak (1990) estimated annual food consumption to biomass ratios for Barents Sea deep-water redfish (*Sebastes mentella*) that varied from a high of 6.0 yr⁻¹ for fingerlings down to around 1.3 yr⁻¹ for fish of 19 years of age. Since fingerlings and very young fish did not make up a significant part of the biomass, the mean Q/B of fish from 10 to 19 years of age was computed. This produced a mean Q/B ratio of 1.490 yr⁻¹. In another study on redfish from west Greenland, it was determined that daily rations were 0.46% and 0.86% of body mass for the autumn–winter and spring–summer periods, respectively (Pedersen and Riget 1992b). These two values were averaged, which gave a mean of 0.66% body mass per day and was equivalent to a Q/B ratio of 2.409 yr⁻¹. On Georges Bank, the Q/B ratio for redfish was estimated at 7.970 yr⁻¹ (Pauly 1989), while Bundy (2004) used a Q/B of 6.130 yr⁻¹ in the eastern Scotian Shelf. Finally, we estimated a Q/B of 3.703 yr⁻¹ from the study of Laurinolli et al. (2004) on the Scotian Shelf and in the Bay of Fundy. When the minimum and maximum biomass values and the previous Q/B ratios were used, we obtained a consumption range of 6.372 to 42.833 t km⁻² yr⁻¹ for redfish. Based on the previous mean production (0.866 t km⁻² yr⁻¹) for redfish and the minimum and maximum GE limits (10–30%), we obtained consumption values of 2.887 and 8.661 t km⁻² yr⁻¹. However, assuming that this species would eat at least as much food as its biomass (Q/B ≥ 1), we used 4.825 t km⁻² yr⁻¹ instead of 2.887 t km⁻² yr⁻¹. The resulting lower and upper consumption limits were 4.825 and 42.833 t km⁻² yr⁻¹, corresponding to a mean consumption of 23.829 ± 26.876 t km⁻² yr⁻¹. The inverse solution estimated a consumption of 4.941 t km⁻² yr⁻¹ for redfish, representing a Q/B of 1.024 yr⁻¹.

For the large demersal feeders, consumption estimates were also derived from different sources (Table 12).

Table 12. Q/B ratios (yr^{-1}) for large demersal feeders. When Q/B ratios were estimated using FishBase (Froese and Pauly 2002), mean length and mass observed during the DFO survey (unpublished data) and a temperature of 3°C were used.

Species	Q/B	Reference
White Hake	3.100	Pauly (1989)
	4.826	Laurinolli et al. (2004) ^a
	3.963	Mean
Black dogfish	2.400	FishBase: 823.70 g and 55.21 cm
Marlin spike	3.900	FishBase: 60.297 g and 27.43 cm
Atlantic halibut	1.400	FishBase: 10,516.73 g and 97.31 cm
Atlantic wolffish	2.100	FishBase: 1,421.64 g and 56.96 cm
	0.450 and 1.770	Blanchard et al. (2002)
	1.325	Laurinolli et al. (2004) ^b
	1.411	Mean
Spotted wolffish	1.600	FishBase: 4,594.14 g and 81.97 cm
	0.450 and 1.770	Blanchard et al. (2002)
	1.273	Mean
Lumpfish	2.200	FishBase: 1,000.31 g and 27.89 cm
Longfin hake	2.600	FishBase: 472.19 g and 39.67 cm
Large eelpout (Zoarcidae)	0.986	Laurinolli et al. (2004) ^c
	2.700 and 5.900 ^d	FishBase: 397.55 g and 43.90 cm
	3.195	Mean
Monkfish	1.800	FishBase: 2,491.29 g and 64.52 cm
	2.455	Laurinolli et al. (2004) ^c
	2.127	Mean

^a: For white hake having a length larger than 35 cm.

^b: For Atlantic wolffish having a length larger than 45 cm.

^c: For large eelpout having a length larger than 35 cm.

^d: The first value is for carnivorous while the second one is for omnivorous fish.

^e: For monkfish having a length larger than 35 cm.

When the annual biomass values for each large demersal species were used and individual consumption values summed, total consumption ranged from 0.248 to $0.746 \text{ t km}^{-2} \text{ yr}^{-1}$. Based on the previous mean production ($0.044 \text{ t km}^{-2} \text{ yr}^{-1}$) for large demersals and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.146 and $0.439 \text{ t km}^{-2} \text{ yr}^{-1}$. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used $0.201 \text{ t km}^{-2} \text{ yr}^{-1}$ instead of $0.146 \text{ t km}^{-2} \text{ yr}^{-1}$. The resulting lower and upper consumption limits were thus 0.201 and $0.746 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean consumption of $0.473 \pm 0.385 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a consumption of $0.245 \text{ t km}^{-2} \text{ yr}^{-1}$ for large demersals, representing a Q/B of 1.217 yr^{-1} .

Consumption estimates for small demersal feeders were derived for juvenile fish from large demersal species (Table 13) and for small demersal species (Table 14).

Table 13. Q/B ratios (yr^{-1}) for large demersal juveniles. When Q/B ratios were estimated using FishBase (Froese and Pauly 2002), mean length and mass observed during the DFO survey (unpublished data) and a temperature of 3°C were used.

Species	Q/B	Reference
White Hake	3.100	Pauly (1989)
	8.264	Laurinolli et al. (2004) ^a
	5.682	Mean
Black dogfish	4.100	FishBase: 65.62 g and 24.53 cm
Marlin spike	5.000	FishBase: 18.84 g and 19.06 cm
Atlantic halibut	2.100	FishBase: 1,241.09 g and 49.49 cm
	3.203	Laurinolli et al. (2004) ^b
	2.652	Mean
Atlantic wolffish	0.450 and 1.770	Blanchard et al. (2002)
	3.900	FishBase: 63.34 g and 20.42 cm
	1.444	Laurinolli et al. (2004) ^c
	1.891	Mean
Spotted wolffish	3.300	FishBase: 135.18 g and 25.42 cm
	0.450 and 1.770	Blanchard et al. (2002)
	1.840	Mean
Lumpfish	4.300	FishBase: 39.12 g and 9.78 cm
Haddock	6.076	Pauly (1989)
	4.630	Blanchard et al. (2002)
	2.947	Mendy and Buchary (2001)
	4.273	Laurinolli et al. (2004) ^d
	4.481	Mean
	3.600	FishBase: 97.98 g and 25.86 cm
Small celpout (Zoarcidae)	1.989	Laurinolli et al. (2004) ^e
	4.400 and 9.600 ^f	FishBase: 35.72 g and 21.48 cm
	5.330	Mean
Monkfish	2.300	FishBase: 914.94 g and 38.60 cm ^g
	4.183	Laurinolli et al. (2004) ^h
	3.242	Mean

^a: For white hake having a length smaller than 35 cm.

^b: For Atlantic halibut having a length smaller than 80 cm.

^c: For Atlantic wolffish having a length smaller than 45 cm.

^d: For haddock having a length smaller than 35 cm.

^e: For small celpout having a length smaller than 35 cm.

^f: The first value is for carnivorous while the second one is for omnivorous fish.

^g: Characteristics of the smallest monkfish; no fish are smaller than 35 cm.

^h: For monkfish having a length smaller than 35 cm.

Table 14. Q/B ratios (yr^{-1}) for small demersal species. When Q/B ratios were estimated using FishBase (Froese and Pauly 2002), mean length and mass observed during the DFO survey (unpublished data) and a temperature of 3°C were used.

Species	Q/B	Reference
Atlantic hagfish	9.700	FishBase: 63.87 g and 38.53 cm
	2.594 and 4.786	Martini et al. (1996)
	5.693	Mean
Fourbeard rockling	4.200	FishBase: 42.92 g and 21.97 cm
Fourline snakeblenny	10.000	FishBase: 30.08 g and 16.04 cm
	5.968	Hutchings (2002)
	7.984	Mean
Blennies (Stichaeidae)	5.400	FishBase: 12.78 g
Soft pout	7.700	FishBase: 2.29 g and 9.96 cm
Sculpins spp.	4.800	FishBase: 22.79 g and 12.86 cm
	6.661	Hutchings (2002)
	5.731	Mean
Sea raven	3.000	FishBase: 209.84 g
	3.878	Laurinolli et al. (2004) ^a
	3.439	Mean
Hookear sculpins	6.400 and 14.000 ^b	FishBase: 5.65 g and 7.96 cm
	10.200	Mean
Triglops spp.	5.700	FishBase: 9.93 g and 11.42 cm
Shorthorn sculpin	2.700	FishBase: 411.18 g and 30.14 cm
Alligatorfish (Agonidae)	6.100	FishBase: 6.88 g and 15.14 cm
	9.100	FishBase: 0.98 g and 8.60 cm ^c
	5.384	Hutchings (2002)
	6.861	Mean
Atlantic spiny lumpsucker	5.300 and 11.600 ^d	FishBase: 14.32 g and 6.20 cm
	8.450	Mean
Snailfish (Liparidae)	5.175	FishBase: 20.40 g and 11.11 cm

^a: For sea raven having a length smaller than 50 cm.

^b: The first value is for Atlantic hookear sculpin while the second is for Arctic hookear sculpin.

^c: Characteristics for Arctic alligatorfish.

^d: The first value is for carnivorous while the second one is for omnivorous fish.

When the annual biomass values for each small demersal species were used and individual consumption values summed, this resulted in a total consumption range of 0.556 to 0.921 t km⁻²

yr⁻¹. Based on the previous mean production (0.170 t km⁻² yr⁻¹) for small demersals and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.568 and 1.704 t km⁻² yr⁻¹. The resulting lower and upper consumption limits were thus 0.556 and 1.704 t km⁻² yr⁻¹, corresponding to a mean consumption of 1.130 ± 0.812 t km⁻² yr⁻¹. The inverse solution estimated a consumption of 1.540 t km⁻² yr⁻¹ for large demersals, representing a Q/B of 5.928 yr⁻¹.

Diet composition

For redfish, we used the diet compositions found by Savenkoff et al. (2005) for the northern Gulf of St. Lawrence (2000–2002), by Bundy (2004) for the eastern Scotian Shelf (1999–2000; n = 137), and by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997) to construct the upper and lower limits used as constraints in inverse modelling for this group (Table 15). The most important prey items of the resulting diet of redfish were shrimp and large zooplankton (72.9% of the diet; Table 15).

For large demersal feeders, very little diet information was available from the northern Gulf during the 2003–2005 period. Stomach content data for Marlin spike (n = 28) and Atlantic halibut (n = 8) were available from 2003 to 2005 (D. Chabot, unpublished data). We also used the diet compositions estimated by Bowman et al. (2000) for the Scotian Shelf, by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s; white hake, n = 1,755), by Bundy (2004) for the eastern Scotian Shelf (1999–2000; haddock [n = 1336], large demersal piscivores [n = 97], and large demersals [n = 63]), and by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997; demersal and benthopelagic piscivores > 40 cm, other large demersals > 30 cm, and lumpfish) to construct the upper and lower limits used as constraints in inverse modelling for this group (Table 15). The most important prey items of the resulting diet of large demersals were large zooplankton, small planktivorous pelagics, small piscivorous pelagics, polychaetes, and small demersals (70.9% of the diet; Table 15).

For small demersal feeders, we used stomach content data for small marlin spike (n = 79), triglops (n = 15), Atlantic soft pout (n = 191), small eelpout (Zoarcidae) (n = 61), small blennies (Stichaeidae) (n = 6), small hookear sculpins (n = 9), sculpins (n = 7), snailfish (Liparidae) (n = 17), and small Atlantic halibut (≤ 80 cm; n = 90) from the northern Gulf during the 2003–2005 period (D. Chabot, unpublished data). We also used the diet compositions estimated by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s; longhorn sculpin [n = 786], shorthorn sculpin [n = 132], and sea raven [n = 67]), by Bundy (2004) for the eastern Scotian Shelf (1999–2000; small demersal piscivores [n = 273], small large demersal [n = 136], and longhorn sculpin [n = 241]), and by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997; demersal and benthopelagic piscivores ≤ 40 cm, other large demersals ≤ 30 cm, and small demersals) to construct the upper and lower limits used as constraints in inverse modelling for this group (Table 15). The most important prey items of the resulting diet of small demersals were large zooplankton, small demersals, small crabs, polychaetes, and small planktivorous pelagics (64.1% of the diet; Table 15).

Table 15. Diet compositions (%) for redfish, large demersal feeders, and small demersal feeders used in modelling. Est: diet estimates from the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Prey	Redfish					Large demersal feeders				
	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	0.1	0.1	0.0	0.2	0.0	5.7	10.8	0.0	38.4	0.1
Large Green. halibut										
Small Green. halibut						1.8	3.1	0.0	11.4	4.9
American plaice						0.8	0.9	0.0	6.8	1.9
Flounders						0.6	0.4	0.0	9.2	0.6
Skates						0.0	0.1	0.0	0.4	0.0
Redfish	0.7	0.5	0.0	2.4	0.7	0.8	1.1	0.0	2.7	2.0
Large demersals						0.1	0.2	0.0	7.3	0.1
Small demersals	0.7	0.6	0.1	1.9	0.1	9.7	10.4	0.0	38.0	1.4
Capelin	5.2	8.4	0.0	21.1	8.0	1.8	3.7	0.0	12.2	7.7
Large pelagics										
Pisci. small pelagics	6.2	6.3	0.3	12.9	0.4	11.0	17.7	0.0	42.1	0.8
Plank. small pelagics	4.8	6.3	0.0	12.1	2.8	19.3	34.4	0.0	87.4	23.3
Shrimp	37.0	29.0	3.5	62.4	20.7	4.7	2.1	0.0	28.6	3.9
Large crabs						0.0	0.0	0.0	1.0	0.0
Small crabs						5.1	8.3	0.0	71.3	1.0
Echinoderms						3.2	4.6	0.0	31.9	5.3
Molluscs	0.0	0.0	0.0	0.0	0.0	0.4	0.4	0.0	2.7	0.4
Polychaetes	0.0	0.0	0.0	0.0	0.0	10.7	16.5	0.0	57.7	18.1
Other bent. inver.	3.8	6.5	0.0	11.3	8.0	3.6	4.8	0.0	18.7	7.8
Large zooplankton	35.9	15.6	23.1	53.8	47.2	20.2	11.8	0.0	80.1	18.6
Small zooplankton	5.7	9.0	0.4	16.1	12.0	0.5	0.9	0.0	5.0	2.1
Phytoplankton										
Detritus										
Total	100.0		27.4	194.1	100.0	100.0		0.0	552.6	100.0
TRN	12					20				

Table 15. Cont.

Prey	Small demersal feeders				
	Mean	± SD	Min	Max	Est
Large cod					
Small cod	1.9	0.8	0.0	14.6	0.0
Large Green. halibut					
Small Green. halibut	0.1	0.3	0.0	2.8	0.1
American plaice	1.5	0.7	0.0	29.1	0.2
Flounders	2.6	1.7	0.0	20.9	0.1
Skates	0.0	0.1	0.0	0.6	0.0
Redfish	1.2	1.0	0.0	9.1	3.0
Large demersals					
Small demersals	8.5	2.3	0.0	31.8	0.1
Capelin	1.0	1.6	0.0	6.1	2.8
Large pelagics					
Pisci. small pelagics	2.3	1.6	0.0	15.2	0.1
Plank. small pelagics	9.2	10.7	0.0	58.1	5.0
Shrimp	13.6	7.0	0.0	34.1	5.2
Large crabs					
Small crabs	10.6	10.3	0.0	86.9	3.0
Echinoderms	4.7	7.1	0.0	34.2	19.3
Molluscs	2.5	2.1	0.0	26.1	12.2
Polychaetes	10.0	4.3	0.0	44.1	10.9
Other bent. inver.	7.6	11.2	0.0	47.2	16.8
Large zooplankton	20.7	17.5	0.0	94.0	16.0
Small zooplankton	1.9	2.4	0.0	70.9	5.2
Phytoplankton					
Detritus					
Total	100.0		0.0	625.7	100.0
TRN	18				

Capelin

Background

Two species were identified and aggregated into the capelin group: capelin (*Mallotus villosus*) and Arctic cod (*Boreogadus saida*). Capelin is a small, short-lived pelagic fish that spends most of its life offshore, moving inshore only to spawn. The species is exploited commercially in some areas and is probably the most important forage fish of the northern Gulf of St. Lawrence (DFO 2001).

The Arctic cod has a circumpolar distribution and is found in the northwest Atlantic from arctic waters in the north down to the southern Gulf of St. Lawrence (Scott and Scott 1988). This species is pelagic and feeds mainly on invertebrates found in the upper part of the water column. Arctic cod is a key component of the marine food web of arctic waters (Hop et al. 1997) and an important link in the transfer of energy from zooplankton to other fish, marine mammals, and seabirds (Lilly et al. 1994). However, because its biomass is generally low in the northern Gulf in recent years, we included it in the capelin group.

Catch

According to the NAFO fisheries statistics (NAFO 2007) and the advisory report (DFO 2006b), the average annual capelin landings for the 2003–2005 period in the study area were 7,168 t or $6.90 \times 10^{-2} \pm 1.71 \times 10^{-2} \text{ t km}^{-2} \text{ yr}^{-1}$. These landings include by-catch values from the shrimp fishery of 2.93×10^{-3} (L. Savard and J. Gauthier, Maurice-Lamontagne Institute, unpublished data). There was no catch data entered in the model for Arctic cod. The inverse solution estimated catch values of $7.00 \times 10^{-2} \text{ t km}^{-2} \text{ yr}^{-1}$ for capelin.

Biomass

Annual biomass estimates of capelin were obtained from the scientific surveys for the 2003–2005 period using the *PACES* software. This resulted in a mean annual biomass estimate of 3,161,834 t or $30.457 \pm 34.414 \text{ t km}^{-2}$ for the 4RS ecosystem. However, the capelin biomass was only a gross approximation (catchability of capelin is unknown and likely variable from year to year for the bottom trawl used on the groundfish survey; in addition, the bottom trawl is very inefficient for estimating the relative abundance/biomass of pelagic species). For Arctic cod, the mean annual biomass estimate was 251 t or $0.002 \pm 0.004 \text{ t km}^{-2}$. The resulting biomass for the capelin group was then $30.460 \pm 34.412 \text{ t km}^{-2}$ (range: 4.074–69.383 t km^{-2}).

Production

There was no information available concerning the P/B ratios of capelin in the study area. Production was assumed to be equal to biomass multiplied by natural mortality (M), plus the catch. Natural mortality was set to 0.63 yr^{-1} to reflect the biology of this short-lived species (F.

Grégoire, Institut Maurice-Lamontagne, pers. comm.) in agreement with the study of Blanchard et al. (2002) in the Barents Sea. When the mean, minimum, and maximum biomass values of the capelin group were used, we obtained a mean annual production of $19.044 \pm 21.832 \text{ t km}^{-2} \text{ yr}^{-1}$ (range: $2.530\text{--}43.797 \text{ t km}^{-2} \text{ yr}^{-1}$). The production value estimated by the inverse solution for capelin was $5.155 \text{ t km}^{-2} \text{ yr}^{-1}$ ($P/B = 0.17 \text{ yr}^{-1}$).

Consumption

Consumption rates for the capelin group were taken from various sources. FishBase (Froese and Pauly 2002) was used to estimate the Q/B ratio assuming a water temperature of 1°C , considering that this species is generally found near the cold intermediate layer in the Gulf of St. Lawrence. This resulted in a Q/B ratio of 4.900 yr^{-1} for fish having a mean mass of 11.89 g and a mean length of 14.0 cm (DFO, groundfish survey database, unpublished data). We used a second estimate based on the feeding ecology of capelin in the estuary and western Gulf of St. Lawrence (Vesin et al. 1981). The daily ration was estimated at 5.00% body mass in summer and 2.50% body mass in winter, giving a mean of 3.75% of body mass per day. From these values, the mean annual Q/B ratio was estimated to be 13.688 yr^{-1} . A third Q/B estimate was determined from a summer study on Barents Sea capelin (Ajiad and Pushaeva 1991). Daily ration was estimated to be between 1.47% and 2.00% of the body mass, resulting in an average Q/B ratio of 6.333 yr^{-1} . In the Barents Sea, Panasenko (1981) estimated a Q/B ratio of 27.558 yr^{-1} while Blanchard et al. (2002) estimated a lower value (4.700 yr^{-1}). Finally, other studies on the consumption of capelin were available: 6.633 yr^{-1} from Mendy and Buchary (2001) for the Icelandic marine ecosystem, 6.570 yr^{-1} from Wilson et al. (2006) for the Gulf of Alaska, 6.880 yr^{-1} from Bundy (2004) for the eastern Scotian Shelf, and 4.644 yr^{-1} from Laurinolli et al. (2004) for the Scotian Shelf and Bay of Fundy. When the biomass values and the previous Q/B ratios were used, we obtained a consumption range of 18.923 to $1912.030 \text{ t km}^{-2} \text{ yr}^{-1}$ for the capelin group.

Based on the previous mean production ($19.044 \text{ t km}^{-2} \text{ yr}^{-1}$) for the capelin group and the minimum and maximum GE limits (10–30%), we obtained consumption values of 63.480 and $190.441 \text{ t km}^{-2} \text{ yr}^{-1}$. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used $30.460 \text{ t km}^{-2} \text{ yr}^{-1}$ instead of $18.923 \text{ t km}^{-2} \text{ yr}^{-1}$. The resulting lower and upper consumption limits were 30.460 and $1912.030 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean annual consumption of $971.245 \pm 1330.471 \text{ t km}^{-2} \text{ yr}^{-1}$. The consumption value estimated by the inverse solution was $35.118 \text{ t km}^{-2} \text{ yr}^{-1}$ ($Q/B = 1.153 \text{ yr}^{-1}$) for capelin.

Diet composition

Stomach content data for capelin from NAFO divisions 4RS were available in 2003 ($n = 1856$; D. Chabot, unpublished data). Large zooplankton and small zooplankton were the main prey (82% and 18%, respectively). However, due to the uncertainty around capelin data, we also used the diet compositions estimated by Jangaard (1974) for the North Atlantic, by Vesin et al. (1981) in the estuary and western Gulf of St. Lawrence, by Bundy (2004) for the eastern Scotian Shelf (1999–2000; $n = 114$), and by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997) to construct the upper and lower limits used as constraints in inverse modelling for

this group (Table 16). The most important prey items of the resulting diet of capelin were large and small zooplankton groups (86.0% of the diet; Table 16).

Table 16. Diet compositions (%) for capelin used in modelling. Est: diet estimates from the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Prey	Capelin				
	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Redfish					
Large demersals					
Small demersals					
Capelin	0.8	1.5	0.0	3.5	1.6
Large pelagics					
Pisci. small pelagics					
Plank. small pelagics	0.1	0.2	0.0	0.5	0.1
Shrimp	7.2	16.2	0.0	36.2	1.2
Large crabs					
Small crabs					
Echinoderms					
Molluscs					
Polychaetes	5.9	13.1	0.0	29.3	7.2
Other bent. inver.	0.0	0.0	0.0	0.0	0.0
Large zooplankton	54.0	19.2	30.9	85.2	50.5
Small zooplankton	32.0	22.6	0.0	55.1	39.4
Phytoplankton					
Detritus					
Total	100.0		30.9	209.8	100.0
TRN	7				

Pelagic feeders

Background

The pelagic feeders are also an important part of the ecosystem, and some species are commercially fished. Three groups are designed to represent these species: large pelagic feeders, piscivorous small pelagic feeders, and planktivorous small pelagic feeders.

The large pelagic feeders include silver hake (*Merluccius bilinearis*), pollock (*Pollachius virens*), and spiny dogfish (*Squalus acanthias*). The most abundant large pelagic feeder in NAFO divisions 4RS is silver hake (41% of biomass). Juveniles of these species were classified as either piscivorous or planktivorous small pelagic feeders according to juvenile feeding behaviour.

The piscivorous small pelagic feeders include Atlantic mackerel (*Scomber scombrus*), short-finned squid (*Illex illecebrosus*), white barracudina (*Arctozenus risso*), and juveniles of large pelagics. Atlantic mackerel was the most important in terms of biomass (97%) and was therefore considered the key species for the group. Mackerel populations in the northwest Atlantic form a stock complex that overwinters off the New England coast. A part of this stock complex then migrates northwards in May and June to spawn in the southern Gulf of St. Lawrence (Moores et al. 1975). After spawning, they disperse throughout the Gulf for the rest of the summer (DFO 2003b).

The planktivorous small pelagic feeders include Atlantic herring (*Clupea harengus*), Atlantic argentine (*Argentina silus*), planktivorous myctophids, sand lance (*Ammodytes* spp.), and other mesopelagics. Atlantic herring was the most important in terms of biomass (99%) and was therefore considered the key species for the group. The herring population in the northeast Gulf consists of two stocks, one spawning in spring and one in the fall, with July 1st as the separation date for their spawning seasons. The spring-spawning population congregates off the west coast of Newfoundland and in and around St. George's Bay; the autumn-spawning stock regroups further up the coast, north of Point Riche, to reproduce (McQuinn et al. 1999). Outside of the spawning season, these two stocks are mainly found in St. George's Bay in the spring, north of Point Riche and in the Strait of Belle Isle in the summer, and off Bonne Bay in the fall (McQuinn et al. 1999).

Catch

For the large pelagic feeders, landings for pollock and silver hake were 2 t or 1.93×10^{-5} t km⁻² yr⁻¹ (SD = 2.72×10^{-5} t km⁻² yr⁻¹) (NAFO 2007). The inverse solution estimated a catch value of 2.53×10^{-5} t km⁻² yr⁻¹.

The mean landings of piscivorous small pelagic feeders in NAFO divisions 4RS for 2003–2005 were 21,330 t or 2.05×10^{-1} t km⁻² yr⁻¹ (SD = 6.06×10^{-2} t km⁻² yr⁻¹), mostly (99% of the total landings) attributable to Atlantic mackerel and shortfin squid (NAFO 2007). The inverse solution estimated a catch value of 2.10×10^{-1} t km⁻² yr⁻¹.

For the planktivorous small pelagic feeders, landings for Atlantic herring (the only species for which data were available) were 15,986 t or 1.54×10^{-1} t km⁻² yr⁻¹ (SD = 1.46×10^{-2} t km⁻² yr⁻¹) (NAFO 2007). The inverse solution estimated a catch value of 1.57×10^{-1} t km⁻² yr⁻¹.

Biomass

For the large pelagic feeders, biomass was calculated from scientific research survey data covering NAFO divisions 4RS during the 2003–2005 period. Biomass estimates were only available for silver hake, pollock, and spiny dogfish. The biomasses of all three species were then summed to obtain an estimate for the group. The mean biomass for the large pelagic feeders was estimated to be 667 t or 0.006 t km^{-2} ($\text{SD} = 0.005 \text{ t km}^{-2}$; range: $0.003\text{--}0.010 \text{ t km}^{-2}$).

Biomass estimates for Atlantic mackerel were derived from an egg production index calculated for 1983 to 2005 for the southern Gulf of St. Lawrence according to the method described in DFO (2003b). We did not apply a residence time factor to reduce biomass by two (6 months outside the Gulf) because this kind of fish feeds mainly during the summer period when they are in the Gulf. Only the 2003–2005 estimates were used to calculate the mean annual biomass. After spawning, mackerel disperse throughout the entire area (NAFO divisions 4RS and 4T). There is a little information about the proportion of mackerel that moves into the northern (4RS) versus southern (4T) Gulf. We assumed that one third of the biomass moved into 4RS while the other two thirds were distributed in 4T. Knowing that the northern Gulf represents 59.7% of the trawlable surface area of the entire Gulf of St. Lawrence, mackerel biomass was estimated to be 39,924 t or 0.385 t km^{-2} ($\text{SD} = 0.309 \text{ t km}^{-2}$). All the other small piscivorous pelagic biomasses were evaluated from scientific research survey data but were very low. For the whole group, biomass was estimated to be $0.395 \pm 0.303 \text{ t km}^{-2}$ (range: $0.181\text{--}0.609 \text{ t km}^{-2}$).

For the planktivorous small pelagic feeders, the average biomass of herring (the key species for the group) in 2003 in the eastern part of the study area (NAFO division 4R) was taken from the sequential population analysis (SPA) (Grégoire et al. 2004). The total biomass was 107,402 t or 1.035 t km^{-2} in 2003. There has been no acoustic survey to measure the abundance of the two herring spawning stocks of the west coast of Newfoundland since 2002. Without an abundance survey, there is no analytical assessment (SPA) and thus no biomass estimates. Also, data for herring populations in 4S were unavailable. However, based on newly acquired data and fishery observations (the presence of large fish and strong year-classes that have been observed in the gillnet fishery for many years; bays with milky white opaque and creamy water from enormous spawn), we thought that it was better to attempt, to the best of our ability, to estimate the 4S biomass than to ignore it. Even though the survey gear is considered inefficient for estimating relative pelagic fish biomass/abundance, we decided to use biomasses of herring and other small planktivorous pelagic species that were evaluated from research survey data. The resulting biomass values were 19,969 t or $0.192 \text{ t km}^{-2} \text{ yr}^{-1}$ in 2003 and 693,836 t or $6.684 \text{ t km}^{-2} \text{ yr}^{-1}$ 2005 (no survey in 2004). This range is large and we decided to use these values as guesstimates for biomass limits. Mean biomass for the planktivorous small pelagic group was $3.438 \pm 4.590 \text{ t km}^{-2}$.

Production

There was no information on specific P/B ratios for the large pelagic feeders in the study area. Based on Bundy (2004), we estimated a P/B of 0.890 yr^{-1} for silver hake (mean of two values 0.845 and 0.934 yr^{-1}) and 0.306 yr^{-1} for pollock. There are no direct estimates of

production of spiny dogfish. Production was estimated by multiplying biomass by natural mortality (M), plus catch, assuming a natural mortality of 0.200 yr^{-1} (Bundy 2004). For spiny dogfish, we used also a P/B of 0.400 yr^{-1} estimated by Bundy et al. (2000) for the large pelagic feeder group on the Newfoundland–Labrador Shelf. When the annual biomass values for each species were used and individual production values summed, we obtained a production range of 0.001 to $0.006 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean production of $0.003 \pm 0.004 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a production of $0.006 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a P/B of 0.887 yr^{-1} .

For the piscivorous small pelagic feeders, a value of 0.2 yr^{-1} was used for natural mortality in the absence of better information (F. Grégoire, DFO, Institut Maurice-Lamontagne, pers. comm.). For squid, a value of 1.0 yr^{-1} was used for natural mortality. For silver hake juveniles (no biomass values for the other piscivorous juvenile large pelagics), we used a P/B of 0.957 yr^{-1} (mean of two values 0.845 and 1.069 yr^{-1}) from Bundy (2004). When the annual biomass values for each species were used and individual production values summed, we obtained a production range of 0.184 to $0.376 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean of $0.280 \pm 0.136 \text{ t km}^{-2} \text{ yr}^{-1}$. However, based on initial inverse modelling runs, the previous values seemed to be too low to meet predator demands. A production of $0.507 \text{ t km}^{-2} \text{ yr}^{-1}$ (35% increase) was required and was thus used as the maximum production limit. The resulting lower and upper production limits were thus 0.184 to $0.507 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean of $0.345 \pm 0.229 \text{ t km}^{-2} \text{ yr}^{-1}$. This mean production value was related to a biomass value of 0.488 t km^{-2} , which is included in the observed biomass range (see the previous biomass section). The production value estimated by the inverse solution was $0.504 \text{ t km}^{-2} \text{ yr}^{-1}$ (P/B = 1.27 yr^{-1}) for piscivorous small pelagic feeders.

For the planktivorous small pelagic feeders, production was estimated by multiplying biomass by natural mortality (M), plus catch. Natural mortality was assumed to be 0.2 yr^{-1} (Grégoire and Lefebvre 2002). When the minimum and maximum biomass values were used, we obtained a production range of 0.186 to $1.507 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean production of $0.847 \pm 0.934 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a production of $1.331 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a P/B of 0.39 yr^{-1} .

Consumption

For the large pelagic feeders, consumption estimates were derived from different sources (Table 17).

Table 17. Q/B ratios (yr^{-1}) for large pelagic feeders.

Species	Q/B	Reference
Spiny dogfish	4.770	Pauly (1989)
	4.745	Wetherbee and Cortès (2004)
	2.500	Tanasichuck et al. (1991)
	2.700	Jones and Geen (1977)
	2.051	Laurinolli et al. (2004) ^a
	3.353	Mean
Pollock	4.760	Pauly (1989)
	2.560	Okey and Wright (2004)
	3.590	Bundy (2004)
	9.516	Cohen and Grosslein (1981)
	4.685	Mean
Silver hake	3.850 and 4.260	Pauly (1989)
	7.869	Durbin et al. (1983)
	11.315	Edwards and Bowman (1979)
	7.605	Cohen and Grosslein (1981)
	6.525	Laurinolli et al. (2004) ^b
	5.500	Bundy (2004)
	4.161	Waldron (1988)
	6.386	Mean

^a: For spiny dogfish having a length larger than 70 cm.

^b: For silver hake having a length larger than 35 cm.

When the annual biomass values for each large pelagic species were used and individual consumption values summed, total consumption ranged from 0.013 to 0.052 $\text{t km}^{-2} \text{yr}^{-1}$. Based on the mean production (0.003 $\text{t km}^{-2} \text{yr}^{-1}$) for the large pelagic feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.012 and 0.035 $\text{t km}^{-2} \text{yr}^{-1}$. The resulting lower and upper consumption limits were 0.012 and 0.052 $\text{t km}^{-2} \text{yr}^{-1}$, corresponding to a mean consumption of $0.032 \pm 0.029 \text{ t km}^{-2} \text{yr}^{-1}$. The inverse solution estimated a consumption of 0.029 $\text{t km}^{-2} \text{yr}^{-1}$ for the large pelagic feeders, representing a Q/B ratio of 4.446 yr^{-1} .

For the piscivorous small pelagic feeders, consumption estimates were derived from different sources (Table 18).

Table 18. Q/B ratios (yr^{-1}) for piscivorous small pelagic feeders.

Species	Q/B	Reference
Atlantic mackerel	4.400	Pauly (1989)
	2.190	Mehl and Westgard (1983) ^a
	1.574	Laurinolli et al. (2004)
	2.270	Blanchard et al. (2002)
	1.767	Bundy et al. (2001)
	2.200	Bundy (2004)
	2.400	Mean
Shortfin squid	2.940	Maurer and Bowman (1985)
Silver hake juveniles	3.850 and 4.260	Pauly (1989)
	7.869	Durbin et al. (1983)
	11.315	Edwards and Bowman (1979)
	18.722	Laurinolli et al. (2004) ^b
	5.800	Bundy (2004)
	11.607	Waldron (1988)
	9.061	Mean

^a: Mehl and Westgard (1983) estimated mackerel consumption in the North Sea to be 6% of body mass per day ($n = 3,674$). A Q/B ratio of 2.190 yr^{-1} was thus estimated from this information.

^b: For silver hake juveniles having a length smaller than 35 cm.

Using the annual biomass values for each piscivorous small pelagic species and summing individual consumption values, total consumption varied from 0.455 to $1.486 \text{ t km}^{-2} \text{ yr}^{-1}$. Based on the mean production ($0.345 \text{ t km}^{-2} \text{ yr}^{-1}$) for the piscivorous small pelagic feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 1.151 and $3.453 \text{ t km}^{-2} \text{ yr}^{-1}$. The resulting lower and upper consumption limits were 0.455 and $3.453 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean consumption of $1.954 \pm 2.120 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a consumption of $2.141 \text{ t km}^{-2} \text{ yr}^{-1}$ for the piscivorous small pelagic feeders, representing a Q/B ratio of 5.417 yr^{-1} .

Consumption estimates of planktivorous small pelagics were derived from different sources (Table 19).

Table 19. Q/B ratios (yr^{-1}) for planktivorous small pelagic feeders.

Species	Q/B	Reference
Atlantic herring	4.590 and 10.100	Pauly (1989)
	2.798	Fetter and Davidjuka (1996) ^a
	13.688	Rudstam et al. (1992) ^b
	5.200	Varpe et al. (2005)
	1.600	Bundy et al. (2001)
	4.840	Blanchard et al. (2002)
	4.723	Mendy and Buchary (2001)
	5.942	Mean
Atlantic argentine	4.367	Laurinolli et al. (2004)
	10.170	Pauly (1989)
	5.584	Ainsworth et al. (2001)
	6.707	Mean
Myctophidae (lanternfishes)	13.000	Froese and Pauly (2002) ^c
	4.800	Heymans and Pitcher (2002)
	8.900	Mean

^a: Fetter and Davidjuka (1996) estimated daily food consumption for different periods of the year. Mean values fluctuated widely between 0.2 and 1.3% of body mass per day, corresponding to an annual Q/B of 2.798 yr^{-1} .

^b: During summer, specific consumption rates of herring in the Baltic Sea were estimated from 10 to 20% of the body mass per day for young-of-the-year fish larger than 5 cm, 7 to 13% for 1+ fish, and 4 to 5% for older age groups (Rudstam et al. 1992). During autumn, these consumption rates declined to 2 to 4% for all age classes. This resulted in an estimated annual Q/B of 13.688 yr^{-1} .

^c: At 3°C for black dogfish having a mean mass of 8.38 g and a mean length of 12 cm (DFO, groundfish survey database, unpublished data).

When the annual biomass values for each planktivorous small pelagic species were used and individual consumption values summed, total consumption ranged from 1.147 to $39.722 \text{ t km}^{-2} \text{ yr}^{-1}$. Based on the mean production ($0.847 \text{ t km}^{-2} \text{ yr}^{-1}$) for the planktivorous small pelagic feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 2.823 and $8.468 \text{ t km}^{-2} \text{ yr}^{-1}$. However, assuming that this species would eat at least as much food as its biomass ($\text{Q/B} \geq 1$), we used $3.438 \text{ t km}^{-2} \text{ yr}^{-1}$ instead of $1.147 \text{ t km}^{-2} \text{ yr}^{-1}$. The resulting lower and upper consumption limits were 3.438 and $39.722 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean consumption of $21.580 \pm 25.657 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a consumption of $6.315 \text{ t km}^{-2} \text{ yr}^{-1}$ for the planktivorous small pelagic feeders, representing a Q/B ratio of 1.837 yr^{-1} .

Diet composition

Diet data from NAFO divisions 4RS during the 2003–2005 period were unavailable for the large pelagic feeders, so studies from other areas and time periods were used instead. We used the diet compositions estimated by Bowman et al. (2000) for the Gulf of Maine, by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s; spiny dogfish, $n = 48$), by Bundy (2004) for the eastern Scotian Shelf (1999–2000; silver hake [$n = 33$], pollock [$n = 141$], and spiny dogfish [82]), and by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997; spiny dogfish and transient pelagics) to construct the upper and lower limits used as constraints in inverse modelling for this group (Table 20). The most important prey items of the resulting diet of large pelagics were small planktivorous pelagics, small piscivorous pelagics, and large zooplankton (78.2% of the diet; Table 20).

For piscivorous small pelagic feeders, we used stomach content data for mackerel ($n = 589$) and white barracudina ($n = 180$) from the northern Gulf during the 2003–2005 period (D. Chabot, unpublished data). We also used the diet composition estimated by Darbyson et al. (2003) in the southern Gulf (mackerel, $n = 265$), by Savenkoff et al. (2004c) for the southern Gulf (mid-1990s; mackerel [$n = 515$]), and by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997; transient mackerel > 29 cm, small mesopelagics, and shortfin squid) to construct the upper and lower limits used as constraints in inverse modelling for this group (Table 20). The most important prey items of the resulting diet of piscivorous small pelagics were small zooplankton, large zooplankton, capelin, and small planktivorous pelagics (91.9% of the diet; Table 20).

For the diet of the planktivorous small pelagic feeders, we used the diet composition estimated by Darbyson et al. (2003) in the southern Gulf, by Savenkoff et al. (2004c) for the southern Gulf (mid-1990s; herring [$n = 718$]), by Bundy (2004) for the eastern Scotian Shelf (1999–2000; sand lance and mesopelagics), and by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997; herring, sand lance, and small pelagics) to construct the upper and lower limits used as constraints in inverse modelling for this group (Table 20). The most important prey items of the resulting diet of small planktivorous pelagics were small and large zooplankton (94.0% of the diet; Table 20).

Table 20. Diet compositions (%) for large pelagic feeders, piscivorous small pelagic feeders, and planktivorous small pelagic feeders used in modelling. Est: diet estimates from the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Prey	Large pelagic feeders					Piscivorous small pelagic feeders				
	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	0.4	0.5	0.0	2.0	0.4	1.8	3.6	0.0	21.5	0.0
Large Green. halibut										
Small Green. halibut	0.0	0.1	0.0	0.3	0.0					
American plaice	1.1	2.3	0.0	14.2	6.7	0.0	0.0	0.0	0.0	0.0
Flounders	1.8	3.5	0.0	7.2	5.9	0.0	0.0	0.0	0.0	0.0
Skates	0.0	0.1	0.0	5.2	0.0					
Redfish	2.0	2.4	0.0	8.4	4.4					
Large demersals										
Small demersals	2.9	2.3	0.0	6.2	0.0	0.1	0.1	0.0	0.2	0.1
Capelin	4.1	5.3	0.0	36.6	14.0	19.4	13.5	0.0	55.0	14.0
Large pelagics										
Pisci. small pelagics	18.0	13.1	0.0	37.3	3.9	1.0	1.7	0.0	6.5	0.0
Plank. small pelagics	45.2	32.1	12.9	86.3	32.2	13.1	13.8	0.0	45.4	0.1
Shrimp	5.8	5.7	0.0	17.5	6.8	2.2	4.3	0.0	80.6	5.6
Large crabs	0.0	0.0	0.0	1.1	0.0					
Small crabs	0.1	0.1	0.0	1.1	0.1					
Echinoderms										
Molluscs										
Polychaetes	1.4	2.0	0.0	4.5	2.4	0.0	0.0	0.0	0.0	0.0
Other bent. inver.	2.1	3.0	0.0	17.9	6.7	3.1	4.7	0.0	30.0	9.0
Large zooplankton	14.9	12.0	0.0	54.6	16.6	19.6	10.7	0.0	86.8	33.5
Small zooplankton	0.2	0.3	0.0	1.3	0.2	39.8	19.4	0.0	100.0	37.8
Phytoplankton										
Detritus										
Total	100.0		12.9	301.4	100.0	100.0		0.0	426.1	100.0
TRN	17					12				

Table 20. Cont.

Prey	Planktivorous small pelagic feeders				
	Mean	± SD	Min	Max	Est
Large cod					
Small cod	0.0	0.0	0.0	0.0	0.0
Large Green. halibut					
Small Green. halibut					
American plaice	0.0	0.0	0.0	0.0	0.0
Flounders	0.0	0.0	0.0	0.0	0.0
Skates					
Redfish					
Large demersals					
Small demersals	0.0	0.0	0.0	0.0	0.0
Capelin	1.2	2.0	0.0	4.1	0.8
Large pelagics					
Pisci. small pelagics	0.9	1.6	0.0	6.5	0.3
Plank. small pelagics	0.4	0.6	0.0	2.5	0.4
Shrimp	1.8	3.3	0.0	13.7	0.1
Large crabs					
Small crabs					
Echinoderms	0.1	0.1	0.0	0.5	0.1
Molluscs					
Polychaetes					
Other bent. inver.	1.0	1.6	0.0	10.0	5.0
Large zooplankton	36.1	24.8	0.0	93.7	34.9
Small zooplankton	57.9	27.8	0.0	100.0	57.9
Phytoplankton					
Detritus	0.5	1.0	0.0	4.0	0.5
Total	100.0		0.0	235.1	100.0
TRN	13				

Crustaceans

Background

Lobster is not included here because only waters deeper than 37 m were considered. The main crustaceans of the northern Gulf of St. Lawrence ecosystem are shrimp and snow crab. Both are exploited commercially.

The shrimp group consists of several species of penaeid and caridean shrimp and is represented by the key species northern shrimp, *Pandalus borealis*, which dominates the biomass and is fished commercially. Generally, shrimp are found throughout the Estuary and the northern Gulf of St. Lawrence at depths of 150–350 m, but migrations do occur during breeding (the females migrate to shallower waters at the channel heads) and feeding (at night, they leave the ocean floor to feed on small planktonic organisms) (DFO 2002). The striped shrimp (*Pandalus montagui*) and the pink glass shrimp (*Pasiphaea multidentata*) are also found in the northern Gulf but are less abundant.

The snow crab (*Chionoecetes opilio*) represents the key species of the crab group, which also includes other species such as toad crabs (*Hyas* spp.) and rock crab (*Cancer irroratus*). Based on large differences in diet, vulnerability to predation (in particular cannibalism; crab prey ranged between 3.9 and 48.8 mm carapace width, CW), and minimal carapace width of adult snow crabs (40 mm CW), crabs were separated into small (≤ 45 mm CW) and large (> 45 mm CW) categories (Lovrich and Sainte-Marie 1997). Only large crabs are fished and consist almost exclusively of male snow crab ≥ 95 mm CW.

Catch

The annual total landings of shrimp (mainly large $[\geq 22$ mm carapace length] female *Pandalus borealis*) were 24,087 t or $2.98 \times 10^{-1} \text{ t km}^{-2} \text{ yr}^{-1}$ ($\text{SD} = 3.90 \times 10^{-2} \text{ t km}^{-2} \text{ yr}^{-1}$) from 2003 to 2005 (NAFO 2007). The small shrimp (< 22 mm CL), mainly juvenile and male *P. borealis* and individuals from other shrimp species, are only partially recruited to the fishery (Savard and Bouchard 2004). The inverse solution estimated catch values of $3.03 \times 10^{-1} \text{ t km}^{-2} \text{ yr}^{-1}$ for shrimp.

For large crabs, a mean of 5,258 t was taken annually between 2003 and 2005, resulting in total landings of $5.07 \times 10^{-2} \text{ t km}^{-2} \text{ yr}^{-1}$ ($\text{SD} = 2.67 \times 10^{-3} \text{ t km}^{-2} \text{ yr}^{-1}$) (snow crabs: 94% of total landings; NAFO 2007). No catch values have been recorded for small crabs. The inverse solution estimated a catch value of $5.07 \times 10^{-2} \text{ t km}^{-2} \text{ yr}^{-1}$ for large crabs.

Biomass

Shrimp biomass was calculated from scientific research survey data covering NAFO zones 4RS during the 2003–2005 period taking into account diurnal variation in catch rate (L. Savard, Institut Maurice-Lamontagne, pers. comm.). For the shrimp group, biomass was 265,064 t or $2.665 \pm 0.568 \text{ t km}^{-2}$ (range: 2.264–3.067 t km^{-2} ; northern shrimp: 99.6% of total biomass).

Current snow crab assessments do not estimate the total biomass in the Gulf of St. Lawrence. Biomass for the crab groups was estimated using the abundance of snow crabs estimated by a complete bottom trawl survey conducted in Baie Sainte-Marguerite (B. Sainte-Marie, Institut Maurice-Lamontagne, unpublished data) in 1992 (period of low abundance of small crabs) and 2003–2005 in order to have extreme values representing potential ranges of the biomass for the crab groups in the whole northern Gulf. Abundance values were converted into biomass values using carapace width and biomass relationships for female, male, and immature crabs for the two size classes (B. Sainte-Marie, Institut Maurice-Lamontagne, unpublished data). Assuming that size structure and biomass density were similar throughout the Gulf for areas shallower than 200 m depth ($103,812 - 57,858 = 45,954 \text{ km}^2$; $57,858 \text{ km}^2$ represents the area deeper than 200 m depth according to the "Petrie box" area in Gilbert et al. [1995]), we obtained a mean biomass estimate of $3.257 \pm 2.318 \text{ t km}^{-2}$ (range: $1.618\text{--}4.896 \text{ t km}^{-2}$) and $0.344 \pm 0.217 \text{ t km}^{-2}$ (range: $0.190\text{--}0.497 \text{ t km}^{-2}$) for large and small crabs, respectively.

Production

Due to the lack of information, it was assumed that production was equal to biomass multiplied by natural mortality (M), plus the catch. Natural mortality of shrimp was assumed to be 0.64 yr^{-1} (Fr chette and Labont  1981). We also used the mean P/B ratio (1.45 yr^{-1}) obtained by Bundy et al. (2000) for the Newfoundland–Labrador Shelf ecosystem. The two methods resulted in a mean production of $2.925 \pm 1.206 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a production of $3.934 \text{ t km}^{-2} \text{ yr}^{-1}$ ($P/B = 1.48 \text{ yr}^{-1}$) for the shrimp group.

For large and small crabs, assumed natural mortality values of 0.2 and 0.35 yr^{-1} , respectively, were used to take into account the high natural mortality of juveniles and the lower natural mortality of adults (B. Sainte-Marie, pers. comm.). Using minimum and maximum biomasses, this resulted in a production range of 0.371 to $1.032 \text{ t km}^{-2} \text{ yr}^{-1}$ (mean: $0.702 \pm 0.467 \text{ t km}^{-2} \text{ yr}^{-1}$) for large crabs and 0.067 to $0.174 \text{ t km}^{-2} \text{ yr}^{-1}$ (mean: $0.120 \pm 0.076 \text{ t km}^{-2} \text{ yr}^{-1}$) for small crabs. The inverse solution estimated a production of $0.482 \text{ t km}^{-2} \text{ yr}^{-1}$ ($P/B = 0.15 \text{ yr}^{-1}$) for large crabs and $0.174 \text{ t km}^{-2} \text{ yr}^{-1}$ ($P/B = 0.51 \text{ yr}^{-1}$) for small crabs.

Consumption

In the absence of information on food consumption by northern shrimp, consumption was only estimated by using the gross growth efficiency (GE, the ratio of production to consumption). Based on the mean production ($2.925 \text{ t km}^{-2} \text{ yr}^{-1}$) and the minimum and maximum GE limits (10–30%), we obtained consumption ranges of 9.749 to $29.246 \text{ t km}^{-2} \text{ yr}^{-1}$ (mean: $19.497 \pm 13.787 \text{ t km}^{-2} \text{ yr}^{-1}$) for shrimp. The inverse solution estimated a consumption of $17.749 \text{ t km}^{-2} \text{ yr}^{-1}$ ($Q/B = 6.659 \text{ yr}^{-1}$).

Snow crab consumption data were obtained from a study conducted in the baie des Chaleurs and the southern Gulf of St. Lawrence (Br thes et al. 1984). A daily ration of 0.4% of body mass was estimated, resulting in a Q/B ratio of 1.460 yr^{-1} . A second estimate was derived from a study of the physiological energetics of the snow crab (Thompson and Hawryluk 1990). The estimated Q/B ratio was 1.302 yr^{-1} . When the minimum and maximum biomass values for

each crab group and the two previous Q/B ratios were used, we obtained a consumption range of 2.106 to 7.148 t km⁻² yr⁻¹ for large crabs and 0.248 to 0.725 t km⁻² yr⁻¹ for small crabs. Based on the minimum and maximum production values for each crab group and the minimum and maximum GE limits (10–30%), we obtained consumption ranges of 1.237 to 10.319 t km⁻² yr⁻¹ for large crabs and 0.222 to 1.739 t km⁻² yr⁻¹ for small crabs. The resulting consumption ranges were 1.237 to 10.319 t km⁻² yr⁻¹ (mean: 5.778 ± 6.422 t km⁻² yr⁻¹) for large crabs and 0.222 to 1.739 t km⁻² yr⁻¹ (mean: 0.980 ± 1.073 t km⁻² yr⁻¹) for small crabs. The inverse solution estimated a consumption of 4.809 t km⁻² yr⁻¹ (Q/B = 1.477 yr⁻¹) for large crabs and 1.241 t km⁻² yr⁻¹ (Q/B = 3.613 yr⁻¹) for small crabs.

Diet composition

For shrimp, feeding occurs in both the benthic and pelagic environments as a result of their daily vertical migrations. In their model, Bundy et al. (2000) assumed that 30% of the total diet was benthic and 70% was pelagic. Annelids, small crustaceans, detritus, and bottom plants were the main prey during the day while copepods and euphausiids were the principal prey items during the nocturnal migration. We used this diet composition for shrimp (Table 21).

For large crabs, diet data were available from the baie des Chaleurs and the southern Gulf of St. Lawrence (Brêthes et al. 1984) as well as from baie Sainte-Marguerite (Lovrich and Sainte-Marie 1997). Based on Brêthes et al. (1984), abundance estimates were multiplied by the mean mass of each prey to obtain biomass indices for the diet. The main prey items of the 480 snow crabs were polychaetes, gastropods, echinoderms, and decapods. In the stomachs of large snow crabs analyzed by Lovrich and Sainte-Marie (1997), the main prey items were benthic invertebrates (molluscs, polychaetes, and others), shrimp, and small crabs. We also used the diet composition estimated by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence (mid-1990s) and by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997; large crabs > 95 mm CW) to construct the upper and lower limits used as constraints in inverse modelling for this group (Table 22). The most important prey items of the resulting diet of large crabs were molluscs, echinoderms, polychaetes, and detritus (76.3% of the diet; Table 22). For small crabs, we used the diet composition estimated by Lovrich and Sainte-Marie (1997) for baie Sainte-Marguerite and by Pitcher et al. (2002) for the Newfoundland–Labrador Shelf (1995–1997; small crabs ≤ 95 mm CW). The main prey were other benthic invertebrates, molluscs, echinoderms, and large zooplankton (71.0% of the diet) (Table 22).

Table 21. Diet compositions (%) for shrimp used in modelling. Est: diet estimates from the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Prey	Shrimp				
	Mean	\pm SD ^a	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Redfish					
Large demersals					
Small demersals					
Capelin					
Large pelagics					
Pisci. small pelagics					
Plank. small pelagics					
Shrimp	0.0	0.0	0.0	0.0	0.0
Large crabs					
Small crabs					
Echinoderms					
Molluscs					
Polychaetes	1.5	1.6	0.0	3.1	1.1
Other bent. inver.	1.5	2.3	0.0	3.8	3.8
Large zooplankton	12.0	13.6	0.0	25.6	12.8
Small zooplankton	24.0	32.0	0.0	56.0	37.6
Phytoplankton	8.5	8.3	0.2	16.8	15.8
Detritus	52.5	54.2	0.0	100.0	28.9
Total	100.0		0.2	205.3	100.0
TRN	7				

^a: For this group, all the proportions of prey in the diet composition were available only as point estimates. SD was then calculated as $DC_{x \rightarrow y}^{obs} * CV(DC_{x \rightarrow u}^{obs})_{mean}$ ($SD = CV * Mean$), with $DC_{x \rightarrow y}^{obs}$ representing the proportion of prey x consumed by shrimp and $CV(DC_{x \rightarrow u}^{obs})_{mean}$ representing the average of all coefficients of variation of the proportion of prey x consumed by the other groups u of the modelled ecosystem. Min = mean - SD, Max = mean + SD.

Table 22. Diet compositions (%) for large and small crabs used in modelling. Est: diet estimates from the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Prey	Large crabs					Small crabs				
	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod										
Large Green. halibut										
Small Green. halibut										
American plaice										
Flounders										
Skates										
Redfish										
Large demersals										
Small demersals	3.0	4.3	0.0	18.2	0.1	0.6	0.9	0.0	2.5	0.0
Capelin										
Large pelagics										
Pisci. small pelagics										
Plank. small pelagics										
Shrimp	6.4	7.7	2.0	33.3	2.0	2.5	3.5	0.0	5.0	1.8
Large crabs										
Small crabs	7.3	7.6	0.1	44.5	1.0	0.9	1.3	0.0	5.1	0.1
Echinoderms	16.2	9.9	0.0	30.3	27.7	14.3	13.1	5.0	38.5	15.8
Molluscs	30.4	26.6	5.8	69.9	46.8	20.9	5.8	1.8	31.7	30.5
Polychaetes	16.2	10.4	5.5	30.3	10.0	9.1	1.2	2.5	15.4	7.9
Other bent. inver.	4.7	5.0	0.0	12.0	8.0	25.8	15.3	15.0	71.9	21.4
Large zooplankton	1.5	1.0	0.0	2.0	1.3	10.0	14.1	0.0	20.0	8.3
Small zooplankton	0.7	1.0	0.0	2.0	0.0	7.5	10.6	0.0	15.0	6.7
Phytoplankton										
Detritus	13.6	12.9	0.0	31.1	3.0	8.4	4.8	5.0	17.1	7.5
Total	100.0		13.4	273.6	100.0	100.0		29.3	222.2	100.0
TRN	10					10				

Benthic invertebrates

Background

The benthic invertebrates other than shrimp and crabs were divided into four groups: echinoderms, molluscs, polychaetes, and other benthic invertebrates. This last group consisted mainly of miscellaneous crustaceans, nematodes, and other meiofauna. Data were lacking for benthic invertebrates from the northern Gulf of St. Lawrence. Consequently, in many cases it was assumed that benthic biomass ranged between that of the Newfoundland–Labrador Shelf ecosystem (Bundy et al. 2000) and that of the eastern Scotian Shelf (Bundy 2004).

Only part of the mollusc biomass, the soft body tissue, is transferred through the food web. This is confirmed by observations of huge shell beds on the ocean floor (Hutcheson et al. 1981). In order to reduce the biomass and account for soft body tissue only, the ratio of body mass to whole mass of the mollusc *Mesodesma deauratum* was estimated. The mean ratio between blotted wet mass of tissue to whole mass for animals with a shell length between 30 and 35 mm was 0.166 ± 0.023 ($n = 10$; K. Gilkinson, DFO, Northwest Atlantic Fisheries Centre, St. John's, Newfoundland, unpublished data).

Catch

Polychaetes, echinoderms, and other benthic invertebrates were not exploited commercially in the study area during the 2003–2005 period. Only molluscs were commercially harvested. Commercial species are Stimpson clam (*Spisula polynyma*), Iceland scallop (*Chlamys islandica*), sea scallop (*Placopecten magellanicus*), other Pectinidae, and whelks (*Busycon* spp.), species caught at depths > 15 m. Average annual landings were taken from the NAFO statistics and were 3,403 t or $3.28 \times 10^{-2} \text{ t km}^{-2} \text{ yr}^{-1}$ ($\text{SD} = 3.43 \times 10^{-3} \text{ t km}^{-2} \text{ yr}^{-1}$) (NAFO 2007). Using the previous ratio (16.6%) of blotted wet mass of tissue to whole mass for animals, we corrected the previous landings estimated for the whole mass including the shell to landings for soft body tissue only. We obtained $5.44 \times 10^{-3} \pm 5.69 \times 10^{-4} \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a catch value of $5.32 \times 10^{-3} \text{ t km}^{-2} \text{ yr}^{-1}$ for molluscs.

Biomass

The mean biomasses for 4RS were assumed to range between those of the Newfoundland–Labrador Shelf ecosystem (NFLD; Bundy et al. 2000) and those of the eastern Scotian Shelf (ESS; Bundy 2004). The biomass ranges were from 63.700 (ESS) to 112.300 t km^{-2} (NFLD) for echinoderms (mean: $88.000 \pm 34.365 \text{ t km}^{-2}$), 42.100 (NFLD) to 57.400 t km^{-2} (ESS) for molluscs (mean: $49.750 \pm 10.819 \text{ t km}^{-2}$), 10.500 (NFLD) to 11.900 t km^{-2} (ESS) for polychaetes (mean: $11.200 \pm 0.990 \text{ t km}^{-2}$), and 4.900 (ESS) to 7.800 t km^{-2} (NFLD) for other benthic invertebrates (mean: $6.350 \pm 2.051 \text{ t km}^{-2}$).

Production

There is no information available on production estimates of benthic invertebrates in the northern Gulf. All the estimates are taken from the literature for other areas.

Echinoderms

Warwick et al. (1978) estimated an annual production of $0.229 \text{ t km}^{-2} \text{ yr}^{-1}$ ($P/B = 0.343 \text{ yr}^{-1}$) for echinoderms in Carmarthen Bay (South Wales, U.K.) while Buchanan and Warwick (1974) obtained an estimate of $0.108 \text{ t km}^{-2} \text{ yr}^{-1}$ ($P/B = 0.300 \text{ yr}^{-1}$). However, higher echinoderm productions have been reported in the New York Bight ($70.108 \text{ t km}^{-2} \text{ yr}^{-1}$ or $P/B = 1.200$; Steimle 1985) and on Georges Bank ($64.221 \text{ t km}^{-2} \text{ yr}^{-1}$ or $P/B = 1.000$; Steimle 1987). Also, Robertson (1979) estimated an annual P/B of 0.650 yr^{-1} and Jarre-Teichmann and Guénette (1996) used an estimate of 0.600 yr^{-1} on the southern shelf of British Columbia. When the minimum and maximum biomass values were applied to these P/B ratios, we obtained a production range of 19.110 to $134.760 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to an annual production of $60.023 \pm 81.777 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a production of $19.458 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a P/B of 0.221 yr^{-1} .

Molluscs

For molluscs, Warwick et al. (1978) estimated an annual production of $3.824 \text{ t km}^{-2} \text{ yr}^{-1}$ ($P/B = 0.848 \text{ yr}^{-1}$) in Carmarthen Bay (South Wales, U.K.) while Sanders (1956) estimated $4.671 \text{ t km}^{-2} \text{ yr}^{-1}$ ($P/B = 2.135 \text{ yr}^{-1}$) in Long Island Sound. Higher production estimates were reported by Steimle (1985) ($82.121 \text{ t km}^{-2} \text{ yr}^{-1}$ or $P/B = 1.000 \text{ yr}^{-1}$) and by Borkowski (1974) ($23.530 \text{ t km}^{-2} \text{ yr}^{-1}$ or $P/B = 3.830 \text{ yr}^{-1}$). On the other hand, Buchanan and Warwick (1974) reported a lower estimate ($0.600 \text{ t km}^{-2} \text{ yr}^{-1}$). Also, Robertson (1979) estimated an annual P/B of 0.760 yr^{-1} and Jarre-Teichmann and Guénette (1996) used an estimate of 0.700 yr^{-1} on the southern shelf of British Columbia. When the minimum and maximum biomass values were applied to these P/B ratios, we obtained a production range of 29.470 to $219.842 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to an annual production of $73.793 \pm 134.613 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a production of $29.737 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a P/B of 0.598 yr^{-1} .

Polychaetes

Estimates of the annual polychaete production ranged between 0.206 and $74.564 \text{ t km}^{-2} \text{ yr}^{-1}$ ($0.206 \text{ t km}^{-2} \text{ yr}^{-1}$ or $P/B = 1.298 \text{ yr}^{-1}$ in Buchanan and Warwick [1974], $0.939 \text{ t km}^{-2} \text{ yr}^{-1}$ or $P/B = 2.258 \text{ yr}^{-1}$ in Warwick et al. [1978], $5.522 \text{ t km}^{-2} \text{ yr}^{-1}$ or $P/B = 2.050 \text{ yr}^{-1}$ in Sanders [1956], $6.310 \text{ t km}^{-2} \text{ yr}^{-1}$ or $P/B = 2.530 \text{ yr}^{-1}$ in Collie [1987], $8.250 \text{ t km}^{-2} \text{ yr}^{-1}$ or $P/B = 4.300 \text{ yr}^{-1}$ in Peer [1970], $16.050 \text{ t km}^{-2} \text{ yr}^{-1}$ or $P/B = 4.320 \text{ yr}^{-1}$ in Nichols [1975], $21.600 \text{ t km}^{-2} \text{ yr}^{-1}$ or $P/B = 1.090 \text{ yr}^{-1}$ in Curtis [1977], and $74.564 \text{ t km}^{-2} \text{ yr}^{-1}$ or $P/B = 3.000 \text{ yr}^{-1}$ in Steimle [1985]). When the minimum and maximum biomass values were applied to these P/B ratios, we obtained a production range of 11.445 to $51.408 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to an annual production of 29.184

$\pm 28.258 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a production of $18.916 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a P/B of 1.689 yr^{-1} .

Other benthic invertebrates

Estimates of annual production for other benthic invertebrates ranged between 0.517 and $15.677 \text{ t km}^{-2} \text{ yr}^{-1}$ ($0.517 \text{ t km}^{-2} \text{ yr}^{-1}$ or $P/B = 3.400 \text{ yr}^{-1}$ in Shearer [1977], $5.000 \text{ t km}^{-2} \text{ yr}^{-1}$ or $P/B = 4.000 \text{ yr}^{-1}$ in Klein et al. [1975], $15.500 \text{ t km}^{-2} \text{ yr}^{-1}$ or $P/B = 1.650 \text{ yr}^{-1}$ in Cederwall [1977], and $15.677 \text{ t km}^{-2} \text{ yr}^{-1}$ or $P/B = 2.800 \text{ yr}^{-1}$ in Collie [1985]). Also, Mills and Fournier (1979) estimated an annual P/B of 0.250 yr^{-1} on the Scotian Shelf and Jarre-Teichmann and Gu  nette (1996) used an estimate of 0.250 yr^{-1} on the southern shelf of British Columbia. When the minimum and maximum biomass values were applied to these P/B ratios, we obtained a production range of 8.085 to $31.200 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to an annual production of $17.833 \pm 16.345 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a production of $8.503 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a P/B of 1.339 yr^{-1} .

Consumption

In the absence of information on food consumption, consumption values were estimated using a gross growth efficiency (GE) between 0.09 and 0.30 (Christensen and Pauly 1992). For echinoderms, this produced a consumption range between 63.700 and $1,497.333 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean consumption of $780.517 \pm 1,013.732 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a consumption of $82.280 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a Q/B ratio of 0.935 yr^{-1} .

For molluscs, this produced a consumption range between 98.233 and $2,442.689 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean consumption of $1,270.461 \pm 1,657.780 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a consumption of $118.576 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a Q/B ratio of 2.383 yr^{-1} .

For polychaetes, this produced a consumption range between 38.150 and $571.200 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean consumption of $304.675 \pm 376.923 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a consumption of $82.317 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a Q/B ratio of 7.350 yr^{-1} .

For other benthic invertebrates, this produced a consumption range between 26.950 and $346.667 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean consumption of $186.808 \pm 226.074 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a consumption of $40.066 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a Q/B ratio of 6.310 yr^{-1} .

Diet composition

Due to a lack of data in the northern Gulf, diet information for echinoderms was taken from the three most abundant species in NAFO divisions 2J3KL: the sand dollar (*Echinarchnius parma*), the sea urchin (*Strongylocentrotus pallidus*), and the brittle star (*Ophiura robusta*). The resulting diet is 100% detritus (Bundy et al. 2000).

For molluscs, Bundy et al. (2000) analyzed the diet composition of a suspension feeder (*Macoma deauratum*), a deposit feeder (*Macoma calcarea*), and a suspension or detrital feeder (*Liocyma fluctuosa*). Suspension feeders feed on organic detrital matter that is resuspended in the

water immediately above the sediment surface. Deposit feeders can be considered as detrital feeders. Thus, the molluscs are assumed to be detrital feeders of various forms and the diet of the mollusc group is 100% detritus. However, in shallower waters, molluscs can consume phytoplankton (M. Fréchette, Institut Maurice-Lamontagne, pers. comm.). This potential food was also accounted for in the final diet composition (Table 23).

The polychaetes are considered to have a diet of 100% detritus (Nesis 1965, Fauchald and Jumars 1979). However, recent studies at two deeper Laurentian Trough stations (275 and 325 m depth) showed that polychaetes could also consume phytoplankton and that cannibalism could have a significant impact in the diet composition (Desrosiers et al. 2000). The resulting diet is shown in Table 23.

The key organisms for the other benthic invertebrate group are gammarid amphipods. These species feed mainly on organic detritus (Nesis 1965, Hutcheson et al. 1981).

Table 23. Diet compositions (%) for molluscs and polychaetes used in modelling. Est: diet estimates from the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Prey	Molluscs					Polychaetes				
	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod										
Large Green. halibut										
Small Green. halibut										
American plaice										
Flounders										
Skates										
Redfish										
Large demersals										
Small demersals										
Capelin										
Large pelagics										
Pisci. small pelagics										
Plank. small pelagics										
Shrimp										
Large crabs										
Small crabs										
Echinoderms										
Molluscs										
Polychaetes						13.4	16.5	1.8	25.1	10.3
Other bent. inver.										
Large zooplankton										
Small zooplankton										
Phytoplankton	5.0	7.1	0.0	10.0	6.7	43.3	8.2	37.5	49.1	46.7
Detritus	95.0	7.1	90.0	100.0	93.3	43.3	8.2	37.5	49.1	42.9
Total	100.0		90.0	110.0	100.0	100.0		76.7	123.3	100.0
TRN	2					3				

Large zooplankton

Background

Organisms and species representing this group are greater than 5 mm in length and include euphausiids (small [*Thysanoessa raschii* and *T. inermis*] and large [*Meganyctiphanes norvegica*] organisms), chaetognaths (mainly *Sagitta elegans* and *Eukrohnia hamata*), hyperiid amphipods (large [*Themisto libellula*] and small [*T. abyssorum*, *T. gaudichaudi*, and *T. compressa*] organisms), jellyfish (cnidarians [mainly *Aglantha digitalis*, *Dimophyes arctica*, and *Obelia* spp.] and ctenophores [mainly *Beroe* spp.]), mysids (mainly *Boreomysis arctica* and *Mysis mixta*), tunicates, and ichthyoplankton. This group contains omnivorous (most euphausiids, hyperiid amphipods, mysids, and large tunicates) and carnivorous (chaetognaths and jellyfish) species.

Catch

There was no commercial fishery for species in this group during the 2003–2005 period in the northern Gulf.

Biomass

Biomass was calculated from zooplankton data gathered as part of the Atlantic Zonal Monitoring Program in the northern Gulf during the 2003–2005 period from the Sept-Îles, Bonne Bay, Anticosti, and centre Gulf of St. Lawrence transects (M. Harvey, Institut Maurice-Lamontagne, unpublished data). This gives an overall biomass estimate of $9.794 \pm 5.305 \text{ t km}^{-2}$ for the study area.

Production

The production estimate of large zooplankton was obtained from several different sources. These sources included P/B ratios for euphausiids of 4.000 yr^{-1} for the Gulf of St. Lawrence (Berkes 1977), 2.750 yr^{-1} (range: $1.300\text{--}4.200 \text{ yr}^{-1}$; Lindley 1980) to 3.800 yr^{-1} (range: $1.300\text{--}6.300 \text{ yr}^{-1}$; Lindley 1982) for the North Sea, and 1.600 yr^{-1} for the northeast Atlantic off the west coast of Ireland (Mauchline 1985). The resulting mean P/B was 3.038 yr^{-1} for euphausiids. Pauly and Christensen (1996) reported P/B ranges of 2.000 to 4.000 yr^{-1} (mean: 3.000 yr^{-1}) for carnivorous jellies and 1.000 to 3.000 yr^{-1} (mean: 2.000 yr^{-1}) for chaetognaths in mass-balance models of northeastern Pacific ecosystems. For amphipods, Ikeda and Shiga (1999) estimated a daily P/B ratio of 0.016 d^{-1} (or 5.840 yr^{-1}) in Toyama Bay, southern Japan Sea. When the minimum and maximum biomass values were applied to the overall mean P/B ratio (3.469 yr^{-1}), we obtained a production range of 6.765 to $63.439 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean production of $33.980 \pm 40.075 \text{ t km}^{-2} \text{ yr}^{-1}$ for large zooplankton. The inverse solution estimated a production of $48.500 \text{ t km}^{-2} \text{ yr}^{-1}$ (P/B of 4.952 yr^{-1}) for large zooplankton.

Consumption

Consumption was firstly estimated from data on euphausiids in the Gulf of St. Lawrence (mean $Q/B = 11.254 \text{ yr}^{-1}$; Sameoto 1976). Pauly and Christensen (1996) reported a Q/B value of 10.000 yr^{-1} for carnivorous jellies and a Q/B range of 10.000 to 40.000 yr^{-1} for chaetognaths in mass-balance models of northeastern Pacific ecosystems. For chaetognaths, three other values were estimated. First, Kotori (1976) estimated that the carbon requirement of a chaetognath community from the Bering Sea and the north Pacific was $4.71 \text{ mg C m}^{-2} \text{ d}^{-1}$ (or $17.192 \text{ t WW km}^{-2} \text{ yr}^{-1}$) and that the chaetognath biomass was 227 mg C m^{-2} (or $2.27 \text{ t WW km}^{-2}$). A Q/B ratio of 0.021 d^{-1} (or 7.57 yr^{-1}) was thus obtained. Secondly, Feigenbaum (1979) found specific daily rations between 0.08 and 0.12 dry weight basis for chaetognaths in the Gulf Stream, near Miami, corresponding to a mean Q/B ratio of 36.50 yr^{-1} . Finally, Falkenhaus (1991) estimated a mean daily specific ingestion (dry weight basis) of 0.022 d^{-1} in the Barents Sea, corresponding to a Q/B ratio of 8.15 yr^{-1} . The resulting mean Q/B ratio for chaetognaths was 20.44 yr^{-1} . To estimate the Q/B ratio of hyperiid amphipods, two studies were used. Auel and Werner (2003) estimated daily ingestion of $1.9 \pm 0.6\%$ of body carbon per day for the hyperiid amphipod *Themisto libellula* in the Arctic marginal ice zone of the Greenland Sea. Pakhomov and Perissinotto (1996) estimated in situ daily rations equivalent to 6.3% of body dry weight for *Themisto gaudichaudi* in the South Georgia region. The resulting mean Q/B ratio for hyperiid amphipods was 0.041 d^{-1} or 14.97 yr^{-1} . Finally, for mysids, Toda et al. (1987) estimated that ingestion represented 2% body C d^{-1} (equivalent to a Q/B of 0.02 d^{-1} or 7.30 yr^{-1}) at 3°C in lakes while Bowers and Vanderploeg (1982) found ingestion rates of 2 to 6% body weight d^{-1} (equivalent to a Q/B range of 0.02 to 0.06 d^{-1} or 7.30 to 21.90 yr^{-1}) at $5\text{--}11^\circ\text{C}$ in Lake Michigan. The resulting mean Q/B ratio for mysids was 12.17 yr^{-1} . When the minimum and maximum biomass values were applied to the overall mean Q/B ratio (13.766 yr^{-1}), we obtained a consumption range of 26.840 to $251.714 \text{ t km}^{-2} \text{ yr}^{-1}$.

Based on the mean production ($33.980 \text{ t km}^{-2} \text{ yr}^{-1}$) for large zooplankton and the minimum and maximum GE limits (10–30%; Christensen and Pauly 1992), we obtained two other consumption values of 113.268 and $339.803 \text{ t km}^{-2} \text{ yr}^{-1}$. The resulting lower and upper consumption limits were 26.840 and $339.803 \text{ t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean consumption of $183.322 \pm 221.298 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a consumption of $182.616 \text{ t km}^{-2} \text{ yr}^{-1}$ for large zooplankton, representing a Q/B ratio of 18.645 yr^{-1} .

Diet composition

No diet information was available for these species in the northern Gulf of St. Lawrence. In other areas, euphausiids feed on detritus, phytoplankton, chaetognaths, amphipods, and copepods (Mauchline 1980). Pauly and Christensen (1996) reported that the relative proportions of prey in the diet composition of euphausiids in the northeastern Pacific ecosystems were 5% zooplankton, 85% phytoplankton, and 10% detritus. In coastal waters of the northeast Atlantic, Båmstedt and Karlson (1998) found that 23% of *Meganyctiphanes norvegica* (range: 10–44%) and 15% of *Thysanoessa inermis* (range: 0.1–20%) fed carnivorously based on the average values for the highest stomach fullness (1.00) of the krill species. *Calanus finmarchicus* copepodids (stages 2 and 3) were by far the most dominant prey, making up 85 to 95% of the copepod prey mass

(Båmstedt and Karlson 1998). Based on these results, a diet composition for small (*Thysanoessa inermis* and *T. raschii*) and large (*Meganyctiphanes norvegica*) euphausiids may be assumed. Overall proportions of each prey item for the diet composition of the euphausiids were weighted according to the biomass of the small and large euphausiids for the 2003–2005 period (20% and 80%, respectively, of small and large organisms). The most important prey items of the resulting diet of euphausiids were phytoplankton (50%–85%), small zooplankton (8%–39%), detritus (5%–10%), and large zooplankton (0%–2%).

For amphipods, Pauly and Christensen (1996) reported on mass-balance models of northeastern Pacific ecosystems that the relative proportions of each prey were 5% large zooplankton, 90% small zooplankton, and 5% detritus. Shearer and Evans (1975) found that *Parathemisto gaudichaudi* consumed 10.7% copepods, 23.9% decapods, 36.9% chaetognaths, and 33.7% euphausiids. From the Strait of Georgia, Haro-Garay (2003) found that the stomach contents of *Parathemisto pacifica* included 52% copepods, 19% amphipods, 8% cladocera, 7% ostracods, 4% crustacean larvae, 8% diatoms, and 2% euphausiids, while the diet composition of *Cyphocaris challengerii* was 41% amphipods, 33% copepods, 12% cladocera, 4% ostracods, 7% crustacean larvae, and 3% diatoms. Finally, Pakhomov and Perissinotto (1996) found in South Georgia that *Themisto gaudichaudi* fed 12% on euphausiids, 3.4% on chaetognaths, and 83.8% on small zooplankton. The most important prey items of the resulting diet of amphipods were small zooplankton (29%–90%), large zooplankton (0%–100%), phytoplankton (0%–8%), and detritus (0%–5%).

The mysid species feed mainly on organic detritus (100% detritus). *Boreomysis arctica* is probably a filter-feeder, consuming phytodetritus, although it also feeds on crustacean carcasses (Cartes and Sorbe 1998).

For chaetognaths, Pauly and Christensen (1996) reported that mesozooplankton accounted for 100% of the diet composition in northeastern Pacific ecosystems. Small prey such as tintinnids and rotifers may be important in the diet of young chaetognaths (Pearre 1981), but the main diet consists of copepod nauplii and copepodid stages (Sameoto 1987, Tonnesson and Tiselius 2005). Barnacle nauplii, appendicularians, chaetognaths, cladocerans, and fish larvae also contribute to the diet periodically (Tonnesson and Tiselius 2005). Based on the diet composition of *Sagitta enflata* in the western Indian Ocean reported by Øresland (2000 and reference therein; see their Table 1), we estimated that (1) cannibalism accounted for 1% to 3% of the diet, (2) large copepods (including appendicularians [Larvacea]) ranged between 7% and 10% of the diet, and (3) small copepods represented between 54% and 79% of the diet. Sullivan (1980) found that juvenile *Sagitta elegans* mainly prey on small cyclopoid copepods (*Oithona similis*; 86% of the diet in numerical frequency terms) while adults consume larger copepods (50% or more of the diet in numerical frequency terms) at Ocean Station P (Pacific Ocean). The chaetognath *Eukrohnia hamata* consumed significantly more small prey, and 4.1% of the prey of mature *Sagitta elegans* was juvenile chaetognaths (Sullivan 1980). In the Barents Sea, Falkenhaus (1991) found that the diet of adult of *Sagitta elegans* was 53.2% smaller mesozooplankton prey, 40.7% larger mesozooplankton prey, and 6.2% unidentified prey in terms of proportion of prey number. The most important prey items of the resulting diet of chaetognaths were small zooplankton (38%–100%) and large zooplankton (0%–4%).

For jellies, Pauly and Christensen (1996) reported that the relative proportions of prey were 0% to 33% large zooplankton, 62% to 100% small zooplankton, and 0% to 5% detritus in northeastern Pacific ecosystems.

Due to the uncertainties with diet data, we also used the diet composition found by Bundy et al. (2000) for the Newfoundland–Labrador Shelf. The relative proportions of the prey in the diet were 5% large zooplankton, 43% small zooplankton, 37% phytoplankton, and 15% detritus. The resulting large zooplankton diet is shown in Table 24.

Table 24. Diet composition (%) for large zooplankton used in modelling. Est: diet estimates from the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Prey	Large zooplankton (> 5 mm)				
	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Redfish					
Large demersals					
Small demersals					
Capelin					
Large pelagics					
Pisci. small pelagics					
Plank. small pelagics					
Shrimp					
Large crabs					
Small crabs					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.					
Large zooplankton	31.9	70.7	0.0	100.0	10.0
Small zooplankton	34.6	64.9	8.2	100.0	32.1
Phytoplankton	27.1	60.1	0.0	85.0	50.0
Detritus	6.4	14.1	0.0	20.0	7.9
Total	100.0		8.2	305.0	100.0
TRN	4				

Small zooplankton

Background

The small zooplankton includes zooplankton ≤ 5 mm in length. Larger organisms consisted mainly of calanoid copepods, with *Calanus finmarchicus*, *C. glacialis*, and *C. hyperboreus* dominant in abundance and biomass. The greatest numbers of the *Calanus* spp. were observed in the deeper Laurentian Channel (Roy et al. 2000). The larger organisms also included other copepods (*Metridia* spp. and *Euchaeta norvegica*), larvacea (appendicularians; *Oikopleura* spp. and *Fritillaria borealis*), polychaeta larvae, and isopoda. Smaller organisms were cyclopoid copepods (mainly *Oithona similis* and *Oithona* spp.) and other small copepods (*Pseudocalanus* spp., *Temora longicornis*, and *Microcalanus* spp.). This group also included other organisms such as molluscs (gastropoda: mainly *Limacina helicina*), heterotrophic protozoa (flagellates, dinoflagellates, and ciliates), meroplankton, and tunicates < 5 mm, which are generally underestimated by sampling gear (Strong 1981).

Catch

None.

Biomass

Biomass was calculated from zooplankton data gathered as part of the Atlantic Zonal Monitoring Program in the northern Gulf during the 2003–2005 period from the Sept-Îles, Bonne Bay, Anticosti, and centre Gulf of St. Lawrence transects (M. Harvey, Institut Maurice-Lamontagne, unpublished data). This gives an overall biomass estimate of 85.461 ± 36.683 t km⁻² for the study area.

Production

On the eastern Scotian Shelf, Bundy (2004) estimated a P/B value of 8.400 yr⁻¹ for calanoid copepods (*Calanus finmarchicus*) and 23.000 yr⁻¹ for cyclopoid copepods (*Oithona similis*). The proportion of calanoid copepods was 81% of the small zooplankton biomass (19% for the cyclopoid copepods) in the northern Gulf (M. Harvey, Institut Maurice-Lamontagne, unpublished data). When the minimum and maximum biomass values weighted by the proportions of calanoid and cyclopoid copepods were applied to these P/B ratios, we obtained a production range of 286.877 to 1,794.444 t km⁻² yr⁻¹, corresponding to an annual production of $952.186 \pm 1,066.011$ t km⁻² yr⁻¹. The inverse solution estimated a production of 656.882 t km⁻² yr⁻¹, representing a P/B of 7.686 yr⁻¹.

Consumption

Vézina et al. (2000) estimated a minimum consumption value ($120.04 \text{ mg C m}^{-2} \text{ d}^{-1}$ or $438.135 \text{ t wet mass km}^{-2} \text{ yr}^{-1}$) for the summer and fall periods and a maximum ($425.94 \text{ mg C m}^{-2} \text{ d}^{-1}$ or $1,554.666 \text{ t wet mass km}^{-2} \text{ yr}^{-1}$) value for the winter and spring periods. Based on the mean production ($952.186 \text{ t km}^{-2} \text{ yr}^{-1}$) for small zooplankton and the minimum and maximum GE limits (25–50% Christensen and Pauly 1992), we obtained two other consumption values of 1,904.372 and 3,808.745 $\text{t km}^{-2} \text{ yr}^{-1}$. The resulting lower and upper consumption limits were 438.135 and 3,808.745 $\text{t km}^{-2} \text{ yr}^{-1}$, corresponding to a mean consumption of $2,123.440 \pm 2,383.381 \text{ t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a consumption of $1,537.790 \text{ t km}^{-2} \text{ yr}^{-1}$, representing a Q/B of 17.994 yr^{-1} .

Diet composition

The small zooplankton feed on both autotrophic and heterotrophic microplankton. However, heterotrophic microplankton (heterotrophic dinoflagellates, ciliates, and small metazoans) were included in the small zooplankton group here. Moreover, there is ample empirical evidence that mesozooplankton are omnivorous (Stoecker and Capuzzo 1990, Ohman and Runge 1994, Vézina et al. 2000). Small zooplankton, phytoplankton, and detritus were thus assumed to be potentially accessible to small zooplankton (Table 25).

Table 25. Diet composition (%) for small zooplankton used in modelling. Est: diet estimates from the inverse model; TRN: number of trophic relations; SD: standard deviation. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Prey	Small zooplankton (< 5 mm)				
	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Redfish					
Large demersals					
Small demersals					
Capelin					
Large pelagics					
Pisci. small pelagics					
Plank. small pelagics					
Shrimp					
Large crabs					
Small crabs					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.					
Large zooplankton					
Small zooplankton	50.2	32.3	27.4	73.1	28.5
Phytoplankton	47.2	35.4	22.2	72.2	68.7
Detritus	2.6	3.1	0.4	4.8	2.8
Total	100.0		50.0	150.0	100.0
TRN	3				

Phytoplankton

Background

Diatoms are the most abundant phytoplankton in terms of both cell numbers and biovolumes during spring and winter (Savenkoff et al. 2000). A mixture of autotrophic and mixotrophic organisms including Cryptophytes, diatoms, dinoflagellates, Prasinophytes, and mixotrophic *Strombidium* spp. (in the Spirotrichea) dominated during summer and fall. Prymnesiophytes were important in terms of cell numbers during spring and winter. The diatoms were dominated by *Chaetoceros affinis*, *Chaetoceros* spp., *Leptocylindrus minimus*, and *Thalassiosira nordenskioldii* during winter and by *Thalassiosira* spp. (*T. punctigera*, *T. nordenskioldii*, *T. pacifica*, and *T. bioculata*) and *Fragilariopsis* spp. (*F. oceanica* and *F. cylindrus*) during spring. During summer, the importance of diatoms in the phytoplankton composition was lower, with the majority observed being smaller centric diatoms such as *Minidiscus* sp., *Chaetoceros minimus*, and occasionally larger *Coscinodiscus* spp.

Phytoplankton biomass and production are the only two parameters required for modelling. There is no harvest, and, since they are autotrophs, there is no consumption and no diet.

Biomass

Biomass was calculated from chlorophyll *a* data gathered as part of the Atlantic Zonal Monitoring Program in the northern Gulf during the 2003–2005 period (M. Starr and L. St.-Amand, Institut Maurice-Lamontagne, unpublished data). Phytoplankton biomass is measured as chlorophyll *a* biomass in the 0–100 m surface layer. To facilitate comparisons with other studies in the Gulf of St. Lawrence, phytoplankton carbon biomass was estimated by converting measured chlorophyll *a* concentrations (CHL) to carbon (C) using a C/CHL ratio of 50 (Rivkin et al. 1996, Savenkoff et al. 2000). We then used a conversion factor of 10 g wet mass equal to 1 g C (Christensen and Pauly 1992). The mean biomass for the entire area was $29.957 \pm 15.852 \text{ t km}^{-2}$.

Primary Production

After correcting for phytoplankton respiration ($75 \pm 38 \text{ mg C m}^{-2} \text{ d}^{-1}$), a value of $599 \pm 303 \text{ mg C m}^{-2} \text{ d}^{-1}$ was estimated over the euphotic zone (Savenkoff et al. 2000), giving production rates of $218.55 \pm 110.75 \text{ g C m}^{-2} \text{ yr}^{-1}$ or $2,185.476 \pm 1,107.451 \text{ t km}^{-2} \text{ yr}^{-1}$. The minimum–maximum range was 1,078.025 to 3,292.927 $\text{t km}^{-2} \text{ yr}^{-1}$. The inverse solution estimated a production of 1,575.071 $\text{t km}^{-2} \text{ yr}^{-1}$, representing a P/B of 52.577 yr^{-1} .

Detritus

Background

Detritus represents sinking particulate organic matter including both large particles (consisting of animal carcasses and debris of terrigenous and coastal plants) and fine particles (mostly from planktonic organisms, including feces, moults, phytoplankton aggregates, and bacteria).

Biomass

The detritus mass was estimated using an empirical relationship derived by Pauly et al. (1993) that relates detritus biomass to primary productivity and euphotic depth:

$$(9) \log_{10} D = -2.41 + 0.954 \log_{10} PP + 0.863 \log_{10} E$$

where D is the standing stock of detritus (in g C m^{-2}), PP is primary productivity (in $\text{g C m}^{-2} \text{yr}^{-1}$), and E is the euphotic depth (in m).

The annual value for primary production was $245.9 \pm 109.9 \text{ g C m}^{-2} \text{yr}^{-1}$. The euphotic depth is estimated from Savenkoff et al. (2000) as $28.2 \pm 5.9 \text{ m}$. The primary production estimate and euphotic depth were substituted into equation 9 above, giving a range of detritus biomass estimates from 6.2 to 22.2 g C m^{-2} , or 61.630 to 222.058 t km^{-2} , using a conversion factor of 10 $\text{g wet mass} = 1 \text{ g C}$ (Christensen and Pauly 1992). This resulted in a mean detritus biomass of $132.608 \pm 113.440 \text{ t km}^{-2}$.

Here, bacteria were considered part of the detritus compartment. Detritus estimates had a wide range, and it was assumed that this range should allow for the bacterial biomass (bacterial biomass: $184 \pm 40 \text{ mg C m}^{-2}$ or $1.8 \pm 0.4 \text{ t km}^{-2}$; Savenkoff et al. 2000).

Respiration

Detritus is usually assumed not to respire. However, as bacteria were considered part of the detritus in this study, there would be respiration involved. Based on Savenkoff et al. (2000), we estimated a planktonic respiration (organisms $< 200 \mu\text{m}$ including bacteria) close to $162 \pm 33 \text{ mg C m}^{-2} \text{d}^{-1}$ and $383 \pm 152 \text{ mg C m}^{-2} \text{d}^{-1}$ for the winter–spring and summer–fall periods, respectively, in the euphotic zone of the northern Gulf of St. Lawrence. Vézina et al. (2000) estimated that phytoplankton respiration represented 8 and 20% of the primary production for the winter–spring and summer–fall periods, respectively ($R_{\text{PHY}} = 80 \pm 41 \text{ mg C m}^{-2} \text{d}^{-1}$ for winter–spring and $70 \pm 64 \text{ mg C m}^{-2} \text{d}^{-1}$ for summer–fall). By subtracting, we could estimate a detrital (or bacterial) respiration of $82 \pm 53 \text{ mg C m}^{-2} \text{d}^{-1}$ and $313 \pm 165 \text{ mg C m}^{-2} \text{d}^{-1}$ for the winter–spring and summer–fall periods, respectively. This represented $198 \pm 86 \text{ mg C m}^{-2} \text{d}^{-1}$ or $72 \pm 32 \text{ g C m}^{-2} \text{yr}^{-1}$ for the euphotic zone.

Based on the data collected from July 1992 to June 1994 at three stations located in the Laurentian Channel, Savenkoff et al. (1996) estimated a bacterial respiration of $44 \pm 9 \text{ mg C m}^{-2}$

d^{-1} or $16 \pm 28 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the aphotic layer (up to 300 m depth). By adding bacterial respiration values estimated in the euphotic and aphotic layers, a total detrital respiration could be estimated as $88.3 \pm 42.4 \text{ g C m}^{-2} \text{ yr}^{-1}$ or $882.961 \pm 423.748 \text{ t km}^{-2} \text{ yr}^{-1}$ (range: 459.213–1,306.710 $\text{t km}^{-2} \text{ yr}^{-1}$). The inverse solution estimated a detrital respiration of $769.862 \text{ t km}^{-2} \text{ yr}^{-1}$.

Export

The fraction of the organic carbon that is not returned to the water column but is buried and preserved within the sediment represents the export of detritus. Silverberg et al. (2000) estimated a burial flux of particulate organic carbon between 0.46 and 0.53 $\text{mol C m}^{-2} \text{ yr}^{-1}$ at the Anticosti Gyre and Cabot Strait stations, respectively. This represents a detrital export close to $5.9 \pm 0.6 \text{ g C m}^{-2} \text{ yr}^{-1}$ or $5.94 \times 10^1 \pm 0.59 \times 10^1 \text{ t km}^{-2} \text{ yr}^{-1}$ (range: 5.35×10^1 – $6.53 \times 10^1 \text{ t km}^{-2} \text{ yr}^{-1}$). The inverse solution estimated a detrital export of $5.72 \times 10^1 \text{ t km}^{-2} \text{ yr}^{-1}$.

Data synthesis

Data about biomass, export (here equal to commercial catch), production, and consumption are summarized in Tables 26 and 27.

Table 26. Observed biomass and export for each group used as input parameters for modelling for the 2003–2005 period in the northern Gulf of St. Lawrence. SD: standard deviation, Min: minimum, Max: maximum. Est: value estimated by inverse modelling. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Group	Biomass (t wet mass km ⁻²)				Export (t km ⁻² yr ⁻¹) ^a				
	Value	± SD	Min	Max	Value	± SD	Min	Max	Est.
Mysticeti	0.362	0.160	0.202	0.522					
Odontoceti	0.042	0.018	0.024	0.060	2.10 x 10⁻⁴	9.04 x 10 ⁻⁵	1.46 x 10 ⁻⁴	2.74 x 10 ⁻⁴	2.06 x 10 ⁻⁴
Harp seals	0.151	0.003	0.148	0.153	3.21 x 10 ⁻²	7.67 x 10 ⁻³	2.34 x 10⁻²	3.79 x 10⁻²	2.35 x 10 ⁻²
Hooded seals	0.007	0.000	0.007	0.007					
Grey and harbour seals	0.047	0.003	0.044	0.050	1.95 x 10⁻⁵	3.37 x 10 ⁻⁵	0	5.84 x 10 ⁻⁵	2.93 x 10 ⁻⁵
Seabirds	0.003	0.001	0.002	0.004	2.55 x 10 ⁻⁴	9.63 x 10 ^{-5b}	1.58 x 10⁻⁴	3.51 x 10⁻⁴	1.58 x 10 ⁻⁴
Large cod	0.449	0.073	0.366	0.500	2.44 x 10⁻²	1.67 x 10 ⁻²	3.56 x 10 ⁻³	3.99 x 10 ⁻²	2.80 x 10 ⁻²
Small cod	0.055	0.027	0.030	0.083	6.87 x 10⁻⁵	3.77 x 10 ⁻⁵	2.54 x 10 ⁻⁵	9.36 x 10 ⁻⁵	7.02 x 10 ⁻⁵
Large Green. halibut	0.597	0.052	0.561	0.634	3.67 x 10⁻²	2.03 x 10 ⁻³	3.44 x 10 ⁻²	3.82 x 10 ⁻²	3.65 x 10 ⁻²
Small Green. halibut	1.749	0.974	1.060	2.438	6.95 x 10⁻⁴	1.14 x 10 ⁻⁴	5.85 x 10 ⁻⁴	8.13 x 10 ⁻⁴	6.97 x 10 ⁻⁴
Amer. plaice	0.375	0.114	0.294	0.456	1.46 x 10⁻³	2.35 x 10 ⁻⁴	1.20 x 10 ⁻³	1.66 x 10 ⁻³	1.43 x 10 ⁻³
Flounders	0.066	0.032	0.044	0.089	4.08 x 10⁻³	9.52 x 10 ⁻⁴	3.05 x 10 ⁻³	4.92 x 10 ⁻³	4.21 x 10 ⁻³
Skates	0.079	0.021	0.063	0.094	3.53 x 10⁻⁴	2.21 x 10 ⁻⁴	2.02 x 10 ⁻⁴	6.07 x 10 ⁻⁴	3.84 x 10 ⁻⁴
Redfish	4.825	0.776	4.276	5.374	5.15 x 10⁻³	5.57 x 10 ⁻⁴	4.58 x 10 ⁻³	5.69 x 10 ⁻³	5.25 x 10 ⁻³
Large demersals	0.201	0.148	0.096	0.306	4.08 x 10⁻³	5.68 x 10 ⁻⁴	3.75 x 10 ⁻³	4.74 x 10 ⁻³	3.95 x 10 ⁻³
Small demersals	0.260	0.205	0.115	0.405					
Capelin	30.460	34.412	4.074	69.383	6.90 x 10⁻²	1.71 x 10 ⁻²	5.08 x 10 ⁻²	8.46 x 10 ⁻²	7.00 x 10 ⁻²
Large pelagics	0.006	0.005	0.003	0.010	1.93 x 10⁻⁵	2.72 x 10 ⁻⁵	0	3.85 x 10 ⁻⁵	2.53 x 10 ⁻⁵

Table 26. Cont.

Group	Biomass (t wet mass km ⁻²)				Export (t km ⁻² yr ⁻¹) ^a				
	Value	± SD	Min	Max	Value	± SD	Min	Max	Est.
Pisci. small pel. feeders	0.395	0.303	0.181	0.609	2.05 x 10⁻¹	6.06 x 10 ⁻²	1.36 x 10 ⁻¹	2.50 x 10 ⁻¹	2.10 x 10 ⁻¹
Plank. small pel. feeders	3.438	4.590	0.192	6.684	1.54 x 10⁻¹	1.46 x 10 ⁻²	1.44 x 10 ⁻¹	1.71 x 10 ⁻¹	1.57 x 10 ⁻¹
Shrimp	2.665	0.568	2.264	3.067	2.98 x 10⁻¹	3.90 x 10 ⁻²	2.59 x 10 ⁻¹	3.37 x 10 ⁻¹	3.03 x 10 ⁻¹
Large crabs	3.257	2.318	1.618	4.896	5.07 x 10⁻²	2.67 x 10 ⁻³	4.76 x 10 ⁻²	5.27 x 10 ⁻²	5.07 x 10 ⁻²
Small crabs	0.344	0.217	0.190	0.497					
Echinoderms	88.000	34.365	63.700	112.300					
Molluscs	49.750	10.819	42.100	57.400	5.44 x 10⁻³	5.69 x 10 ⁻⁴	4.99 x 10 ⁻³	6.08 x 10 ⁻³	5.32 x 10 ⁻³
Polychaetes	11.200	0.990	10.500	11.900					
Other benthic invertebrates	6.350	2.051	4.900	7.800					
Large zooplankton	9.794	5.305	1.950	18.285					
Small zooplankton	85.461	36.683	25.748	161.056					
Phytoplankton	29.957	15.852	10.663	65.046					
Detritus	132.608	113.440	61.630	222.058	5.94 x 10 ¹	0.59 x 10 ¹	5.35 x 10¹	6.53 x 10¹	5.72 x 10 ¹

^a: Export was mainly the catch (including the commercial fishery and anthropogenic mortality such as hunting, etc.). For detritus, export was loss of detritus buried as sediment.

^b: calculated as $\text{Exp}_x \cdot \text{CV}(\text{Exp}_y)_{\text{mean}}$ with $\text{CV}(\text{Exp}_y)_{\text{mean}} = 38\%$, the average of all coefficients of variation for observed export.

Table 27. Observed production and consumption used as input parameters for modelling for the 2003–2005 period in the northern Gulf of St. Lawrence. SD: standard deviation, Min: minimum, Max: maximum. Est: value estimated by inverse modelling. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Group	Production (t km ⁻² yr ⁻¹)					Consumption (t km ⁻² yr ⁻¹)				
	Value	± SD	Min	Max	Est.	Value	± SD	Min	Max	Est.
Mysticeti	0.021	0.011	0.014	0.035	0.017	1.762	1.102	0.983	2.541	1.920
Odontoceti	0.006	0.003	0.004	0.009	0.004	0.483	0.290	0.278	0.688	0.421
Harp seals	0.018	0.010	0.011	0.026	0.016	1.234	0.855	0.629	1.838	1.644
Hooded seals	0.0005	0.0003	0.0004	0.0007	0.0007	0.073	0.026	0.055	0.091	0.084
Grey and harbour seals	0.007	0.004	0.004	0.010	0.004	0.423	0.362	0.166	0.679	0.407
Seabirds	0.0008	0.0004	0.0005	0.0011	0.0010	0.450	0.520	0.082	0.817	0.127
Large cod	0.204	0.125	0.116	0.292	0.182	1.357	0.960	0.679	2.036	1.121
Small cod	0.033	0.016	0.018	0.050	0.050	0.205	0.180	0.078	0.332	0.196
Large Green. halibut	0.138	0.006	0.134	0.142	0.136	1.028	0.609	0.597	1.459	0.605
Small Green. halibut	0.875	0.453	0.425	1.464	0.525	8.193	9.113	1.749	14.637	1.762
Amer. plaice	0.111	0.042	0.066	0.168	0.132	1.252	1.240	0.375	2.129	0.533
Flounders	0.024	0.008	0.018	0.030	0.028	0.173	0.131	0.080	0.266	0.143
Skates	0.017	0.005	0.014	0.021	0.020	0.211	0.187	0.079	0.344	0.102
Redfish	0.866	0.320	0.540	1.251	0.540	23.829	26.876	4.825	42.833	4.941
Large demersals	0.044	0.030	0.023	0.065	0.057	0.473	0.385	0.201	0.746	0.245
Small demersals	0.170	0.173	0.048	0.292	0.289	1.130	0.812	0.556	1.704	1.540
Capelin	19.044	21.832	2.530	43.797	5.155	971.245	1330.471	30.460	1912.030	35.118
Large pelagics	0.003	0.004	0.001	0.006	0.006	0.032	0.029	0.012	0.052	0.029

Table 27. Cont.

Group	Production (t km ⁻² yr ⁻¹)					Consumption (t km ⁻² yr ⁻¹)				
	Value	± SD	Min	Max	Est.	Value	± SD	Min	Max	Est.
Pisci. small pel. feeders	0.345	0.229	0.184	0.507	0.504	1.954	2.120	0.455	3.453	2.141
Plank. small pel. feeders	0.847	0.934	0.186	1.507	1.331	21.580	25.657	3.438	39.722	6.315
Shrimp	2.925	1.206	1.708	4.447	3.934	19.497	13.787	9.749	29.246	17.749
Large crabs	0.702	0.467	0.371	1.032	0.482	5.778	6.422	1.237	10.319	4.809
Small crabs	0.120	0.076	0.067	0.174	0.174	0.980	1.073	0.222	1.739	1.241
Echinoderms	60.023	81.777	19.110	134.760	19.458	780.517	1013.732	63.700	1497.333	82.280
Molluscs	73.793	134.613	29.470	219.842	29.737	1270.461	1657.780	98.233	2442.689	118.576
Polychaetes	29.184	28.258	11.445	51.408	18.916	304.675	376.923	38.150	571.200	82.317
Other benthic invertebrates	17.833	16.345	8.085	31.200	8.503	186.808	226.074	26.950	346.667	40.066
Large zooplankton	33.980	40.075	6.765	63.439	48.500	183.322	221.298	26.840	339.803	182.616
Small zooplankton	952.186	1066.011	286.877	1794.444	656.882	2123.440	2383.381	438.135	3808.745	1537.790
Phytoplankton	2185.476	1107.451	1078.025	3292.927	1575.071					

DISCUSSION / CONCLUSION

The present data set was used to construct models of the northern Gulf of St. Lawrence for the 2003–2005 period. Three other reports have been completed for the same area for the mid-1980s (1985–1987: groundfish pre-collapse period), the mid-1990s (1994–1996: groundfish post-collapse period), and the early 2000s (2000–2002: a few years after a limited cod fishery had resumed) (Morissette et al. 2003, Savenkoff et al. 2004b, Savenkoff et al. 2005). The time periods were determined after the analysis of biomass fluctuations for the key fish species of the northern Gulf system (i.e., cod and redfish). Also, these time periods were chosen based on the availability of reliable information for these species.

Ecosystem modelling requires the collection of a considerable amount of information. All parameter estimations were made within a collaborative framework, in which experts for the various functional groups were consulted. This work is the result of a huge effort to assemble data on the biological characteristics of species occurring in the northern Gulf of St. Lawrence during the 2003–2005 period. The validity of any conclusion regarding the ecosystem being studied depends on the input data (and the confidence that we have in them). Even though most of the data are good estimates for the 4RS ecosystem, some input values are rough estimates only (e.g., benthic invertebrates), meaning that these values are assembled from different literature sources and not from independently measured parameters. The quality of the input data was variable. Catch estimates of commercial species are considered quite reliable although there is indirect but reliable evidence for non-negligible fishing mortality that was not accounted for (Fr chet et al. 2006). Biomass estimates for several groups (seals, seabirds, herring, mackerel, crabs) were based on data from other surveys or population models. In other cases, biomass was based on densities reported for other ecosystems (echinoderms, molluscs, polychaetes, and other benthic invertebrates) or was estimated by initial models to meet predator demands (small demersal feeders). Adults of many of the dominant fishes in the northern Gulf ecosystem undertake seasonal migrations between feeding grounds within our study area and overwintering grounds elsewhere. When information was available, biomass was adjusted for residence time (e.g., seals, Atlantic mackerel). However, little feeding occurs on the overwintering grounds (Schwalme and Chouinard 1999), so seasonal migrations out of the study area are of little consequence for our mass-balance models in terms of consumption by these migratory fishes.

Very little is known about fish and invertebrate production and consumption in the Gulf of St. Lawrence. For most model compartments, total mortality was estimated as catch plus biomass multiplied by natural mortality. In these cases, a fixed rate of natural mortality was assumed based on life-history considerations, literature reports, or expert opinion. It was also necessary to use empirical data from other areas and/or time frames (e.g., capelin, shrimp), or less specific information (e.g., pelagic feeders, benthic invertebrates) for production and consumption estimates. Further uncertainties with diet data resulted from assuming that the diet of a key species is representative of the functional group to which it belongs, or from attributing the "unidentified prey" part in stomach content analyses in proportion to the different identified groups in the stomachs. The uncertainties remaining in the understanding of the ecosystem may be due to the use of incorrect values because no data exist or to the confidence limits being too large. They may result from an inaccurate aggregation of species within one functional group or from unknown mechanisms occurring in the ecosystem. This data-collecting process partly explains the high coefficients of variation for the production, consumption, and diet data (71%,

96%, and 167%, respectively) as well as those for biomass and export (51% and 38%, respectively).

Trophic relationships in ecosystems are often studied by describing only one steady-state model, without including parameter uncertainty and the ensuing uncertainty in the interpretation of the results (e.g., Ecopath literature). Here, we used upper and lower limit ranges to constrain the great majority of input data (rather than the means as in Ecopath models). Upper and lower limits were calculated for each input data based on all available field samples and/or literature reports and implying no information on probability distributions or co-variations in the input data. Means and standard deviations were calculated based on all these data within each time period. In other cases, where we had only two extreme values, the mean and half of the range (as SD) were thus calculated. As generally used in box models (Bolin et al. 1983, Metzl et al. 1989, 1990) and inverse models (Jackson and Eldridge 1992, Niquil et al. 1998, Vézina and Savenkoff 1999, Savenkoff et al. 2001, Leguerrier et al. 2003), we applied random perturbations to input data in order to assess the robustness of the solutions. Generally, the parameters are perturbed by $\pm 10\%$ of SD. In our study, the variability of the input data is larger; i.e., the mean coefficients of variation for the input parameters ranged between 38% (export) and 167% (diet proportion) for the 2003–2005 period. Thus, we decided to randomly perturb each term by up to its SD in order to represent the uncertainties of the input data. This procedure allowed us to appraise the uncertainty in the estimated flows given the uncertainties in the input data. In this study, the final solution is always the mean of one solution without perturbation (the “initial solution”) plus 30 iterations with random perturbations of the input data (to a maximum of their standard deviations) to provide an overall view of the ecosystem and to identify robust patterns. Simulated inverse analyses have shown that the general flow structure of ecosystems can be recovered with these techniques, although the details can be inaccurate (Vézina and Pahlow 2003). Our current model, even with 30 compartments, still represents simplifications of the trophic interactions in the northern Gulf of St. Lawrence.

Inverse modelling, as applied here, estimated a large number of parameters, and it is possible that the relatively few data available were insufficient to constrain these parameters. All a posteriori coefficients of variation of the estimated production, consumption, predation, and export values were smaller than the a priori CVs of the observed input data (e.g., parameter sufficiently constrained) (Appendix 5). For respiration, detrital flow, and other mortality causes, the a posteriori CVs were close to the a priori CVs based on observed biomass. However, these a priori CVs should be considered as minimum values since there was no information on uncertainty for these parameters. The reduction from a priori to a posteriori CVs indicates that, among all the possible ways of matching the input data with unknown flows, the analyses retained only those arrangements that meet all the model constraints (narrow the range of possibilities). Several configurations were rejected, i.e., model solutions that included possible values of the parameter (based on a priori CVs) that were incompatible with all the model constraints for all of the flows.

The use of upper and lower limits to constrain the majority of input values (production, consumption, export, and diet composition) and the choice of row and column weights make inverse modelling a flexible tool to quantify mass-balanced flow diagrams and trophic transfer efficiencies that are internally consistent. This is done by finding the solution that minimizes (objective least-square criterion) both the sum of squared flows (thus the total sum of flows through the food web) and the sum of squared residual errors (minimizes the imbalances between

inputs and outputs) consistent with the constraints. This minimum norm (MN) inversion is thought to be a parsimonious solution to the ecosystem flow inverse problem. Vézina et al. (2004) examined different goal functions to solve inverse problems. Although they proposed a new minimization (smoothed norm, SN), which simultaneously minimizes the squared flows and the squared differences between flows, as probably the most attractive option, their simulated experiments also indicated that the MN inversion is a reasonable choice for comparative inverse analyses. However, one problem with the MN inversion is that it can lead to a number of zeros in the flow network (Vézina et al. 2004). This occurs when there are alternative pathways out of a compartment with no a priori constraints on the relative size of these pathways. The associated effect is that many flows are bound to either their upper or lower limits (active constraints). A large number of active constraints suggests that the optimum may not have been found and that the solution was determined by a priori bounds rather than by patterns in the data. In this study, by randomly perturbing data inputs, we constructed a set of 31 balanced iterations and the final solution was the mean of these iterations. Although individual iterations had a large number of active constraints, these varied from iteration to iteration. One realization of the data was thus not sufficient to constrain the model. However, many realizations of the data (mean of different iterations) allowed us to construct a solution that was nearly insensitive to the constraints. Most model estimates fell between the upper and lower limits. Overall, 6% of the constraints were active (Appendix 6). Catch (33%) and ecotrophic efficiency (17%) had the largest proportions of active constraints. Working with averages of many modelling iterations (and their variation) is thus a much stronger approach than to only consider one iteration, and gives more confidence in the results and their interpretation.

Here, the models enabled us to bring together wide-ranging data concerning the northern Gulf ecosystem and produced values that were logically consistent with our model structure and constraints. These values are meaningful in the sense that they meet some clearly imposed constraints that reflect how we think the system is working. However, even though the model was useful in constraining observations into a coherent picture, it remains that the results are sensitive to choices made regarding the modelling structure and that other equivalent solutions are possible. Such a model provides a useful starting point to frame hypotheses about the ecosystem, to identify data gaps, to show where the uncertainties in the food web occur, and to improve the input parameters in order to enhance the quality of future modelling efforts.

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See the CDEENA web site at <http://www.osl.gc.ca/cdeena/en/accueil.shtml>.

REFERENCES

- Ainsworth, C., B. Ferriss, E. Leblond, and S. Gu  nette. 2001. The Bay of Biscay, France: 1998 and 1970 models. *In* Fisheries impacts on North Atlantic ecosystems: models and analyses. Edited by S. Gu  nette, V. Christensen, and D. Pauly. Fisheries Centre Research Reports 9(4), pp. 271-313.
- Ajiad, A. M., and T. Pushaeva. 1991. The daily feeding dynamics in various length groups of the Barents Sea capelin during the feeding period. ICES Council Meeting Papers 1991/H16, 21 pp.
- Allen, K. R. 1971. Relation between production and biomass. Journal of the Fisheries Research Board of Canada 28: 1573-1581.
- Atkinson, D. B., and B. R. Melteff. 1987. The redfish resources off Canada's east coast. *In* Lowell Wakefield Fisheries Symposium: Proceedings of the International Rockfish Symposium, Anchorage, Alaska, USA, October 20-22, 1986, pp. 15-33.
- Auel, H., and I. Werner. 2003. Feeding, respiration and life history of the hyperiid amphipod *Themisto libellula* in the Arctic marginal ice zone of the Greenland Sea. Journal of Experimental Marine Biology and Ecology 296: 183-197.
- B  mstedt, U., and K. Karlson. 1998. Euphausiid predation on copepods in coastal waters of the Northeast Atlantic. Marine Ecology Progress Series 172: 149-168.
- Barlow, J., and P. J. Clapham. 1997. A new birth-interval approach to estimating demographic parameters of humpback whales. Ecology 78: 535-546.
- Barrett, R. T., G. Chapdelaine, T. Anker-Nilssen, A. Mosbech, W. A. Montevecchi, J. B. Reid, and R. R. Veit. 2006. Seabird numbers and prey consumption in the North Atlantic. ICES Journal of Marine Science 63: 1145-1158.
- Berkes, F. 1977. Production of the euphausiid crustacean *Thysano  a rashii* in the Gulf of St. Lawrence. Journal of the Fisheries Research Board of Canada 34: 443-446.
- Blanchard, J. L., J. K. Pinnegar, and S. Mackinson. 2002. Exploring marine mammal-fishery interactions using 'Ecopath with Ecosim': modelling the Barents Sea ecosystem. Science Series Technical Report, CEFAS Lowestoft, 117: 52pp.
- Bolin, B., A. Bj  rkstr  m, K. Holm  n, and B. Moore. 1983. The simultaneous use of tracers for ocean circulation studies. Tellus 35B: 206-236.
- Borkowski, T. V. 1974. Growth, mortality and productivity of south Floridian Littorinidae (*Gastropoda: Prosobranchia*). Bulletin of Marine Science 24: 409-438.
- Boulva, J., and I. A. McLaren. 1979. Biology of the harbor seal, *Phoca vitulina*, in eastern Canada. Bulletin of the Fisheries Research Board of Canada 200, 32 pp.

- Bourdages, H. 2001. Application PACES (Programme d'Analyse des Campagnes d'Échantillonnage Stratifié), Document utilisateur. DFO, Institut Maurice-Lamontagne, Mont-Joli, Québec.
- Bowen, W. D., and G. D. Harrison. 1996. Comparison of harbour seal diets in two inshore habitats of Atlantic Canada. *Canadian Journal of Zoology* **74**: 125-135.
- Bowering, W. R. 1983. Age, growth and sexual maturity of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in the Canadian northwest Atlantic. *Fishery Bulletin* **81**: 599-611.
- Bowering, W. R., and G. R. Lilly. 1992. Greenland halibut (*Reinhardtius hippoglossoides*) off southern Labrador and northeastern Newfoundland (northwest Atlantic) feed primarily on capelin (*Mallotus villosus*). *Netherlands Journal of Sea Research* **29**: 211-222.
- Bowers, J. A., and H. A. Vanderploeg. 1982. *In situ* predatory behavior of *Mysis relicta* in Lake Michigan. *Hydrobiologia* **93**: 121-131.
- Bowman, R. E., C. E. Stillwell, W. L. Michaels, and M. D. Grosslein. 2000. Food of northwest Atlantic fishes and two common species of squid. NOAA Technical Memorandum NMFS-NE **155**: 149 pp.
- Brêthes, J.-C., G. Desrosiers, and F. Coulombe. 1984. Aspects de l'alimentation et du comportement alimentaire du crabe des neiges, *Chionoectes opilio* (O. Fabr.) dans le sud-ouest du golfe du Saint-Laurent (Decapoda, Brachyura). *Crustaceana* **47**: 235-244.
- Brodie, W. B. 1991. An assessment of Greenland halibut in SA2 and Divisions 3KL. NAFO Scientific Council Research Document 91/88, 29 pp.
- Brown, R. G. B. 1986. Revised atlas of eastern Canadian seabirds. I. Shipboard surveys. Ottawa, Canadian Wildlife Service, 111 pp.
- Buchanan, J. B., and R. M. Warwick. 1974. An estimate of benthic macrofaunal production in the offshore mud of the Northumberland coast. *Journal of the Marine Biological Association of the United Kingdom* **54**: 197-222.
- Bundy, A. 2004. Mass balance models of the eastern Scotian Shelf before and after cod collapse and other ecosystem changes. Canadian Technical Report of Fisheries and Aquatic Sciences No. 2520.
- Bundy, A., G. R. Lilly, and P. A. Shelton. 2000. A mass balance model of the Newfoundland-Labrador Shelf. Canadian Technical Report of Fisheries and Aquatic Sciences No. 2310.
- Burton, J. 1980. L'alimentation estivale du fou de Bassan (*Sula bassana* L.) au Rocher aux Oiseaux, Îles-de-la-Madelaine, Québec. *Naturaliste canadien* **107**: 289-291.
- Cairns, D. K. 1981. Breeding, feeding and chick growth of the black guillemot (*Cepphus grylle*) in southern Quebec. *Canadian Field-Naturalist* **95**: 312-318.
- Cairns, D. K., W. A. Montevecchi, V. L. Birt-Friesen, and S. A. Macko. 1990. Energy expenditures, activity budgets, and prey harvest of breeding common murre. *Studies in Avian Biology* **14**: 84-92.
- Cairns, D. K., G. Chapdelaine, and W. A. Montevecchi. 1991. Prey exploitation by seabirds in the Gulf of St. Lawrence. In *The Gulf of St. Lawrence: small ocean or big estuary?* Edited by J.-C. Therriault. Canadian Special Publication of Fisheries and Aquatic Sciences **113**, pp. 227-291.
- Carruthers, E. H., J. D. Neilson, C. Waters, and P. Perley. 2005. Long-term changes in the feeding of *Pollachius virens* on the Scotian Shelf: responses to a dynamic ecosystem. *Journal of Fish Biology* **66**: 327-347.

- Cartes, J., and J. Sorbe. 1998. Aspects of population structure and feeding ecology of the deep-water mysid *Boreomysis arctica*, a dominant species in western Mediterranean slope assemblages. *Journal of Plankton Research* **20**: 2273-2290.
- Caswell, H., S. Brault, A. J. Read, and T. D. Smith. 1998. Harbor porpoise and fisheries: An uncertainty analysis of incidental mortality. *Ecological Applications* **8**: 1226-1238.
- Cederwall, H. 1977. Annual macrofauna production of a soft bottom in the northern Baltic proper. In *Biology of benthic organisms. Edited by B. F. Keegan, P. O. Ceidigh and P. J. S. Boaden*. 11th European Symposium on Marine Biology, Galway (Ireland), 5 Oct 1976, Oxford (UK), Pergamon Press, pp. 155-164.
- Chabot, D., and G. B. Stenson. 2002. Growth and seasonal fluctuation in size and condition of male Northwest Atlantic harp seals *Phoca Groenlandica*: an analysis using sequential growth curves. *Marine Ecology Progress Series* **227**: 25-42.
- Chabot, D., B. Sainte-Marie, K. Briand, and J. M. Hanson. 2008. Atlantic cod and snow crab predator-prey size relationship in the Gulf of St. Lawrence, Canada. *Marine Ecology Progress Series* **363**: 227-240.
- Chapdelaine, G., P. Brousseau, R. Anderson, and R. Marsan. 1985. Breeding ecology of common and Arctic terns in the Mingan Archipelago, Québec. *Colonial Waterbirds* **8**: 166-177.
- Christensen, V., and D. Pauly. 1992. ECOPATH II - A system for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* **61**: 169-185.
- Christensen, V., and D. Pauly (Editors). 1993. Trophic models of aquatic ecosystems. ICLARM Conference Proceedings 26, 390 pp.
- Christensen, V., and D. Pauly. 1998. Changes in models of aquatic ecosystems approaching carrying capacity. *Ecological Applications* **8** (Suppl.): S104-S109.
- Chumakov, A. K., and S. G. Podrazhanskaya. 1986. Feeding of Greenland halibut (*Reinhardtius hippoglossoides*) in the northwest Atlantic. *NAFO Scientific Council Studies* **10**: 47-52.
- Cohen, E., and M. Grosslein. 1981. Food consumption in five species of fish on Georges Bank. *ICES Council Meeting Papers* 1981/G 68, 21 pp.
- Collie, J. S. 1985. Life history and production of three amphipod species on Georges Bank. *Marine Ecology Progress Series* **22**: 229-238.
- Collie, J. S. 1987. Food consumption by yellowtail flounder in relation to production of its benthic prey. *Marine Ecology Progress Series* **36**: 205-213.
- Curtis, M. A. 1977. Life cycles and population dynamics of marine benthic polychaetes from the Disko Bay area of West Greenland. *Ophelia* **16**: 9-58.
- Darbyson, E., D. P. Swain, D. Chabot, and M. Castonguay. 2003. Diel variation in feeding rate and prey composition of Atlantic herring (*Clupea harengus* L.) and Atlantic mackerel (*Scomber scombrus* L.) in the southern Gulf of St. Lawrence. *Journal of Fish Biology* **63**: 1235-1257.
- Desrosiers, G., C. Savenkoff, M. Olivier, G. Stora, K. Juniper, A. Caron, J.-P. Gagné, L. Legendre, S. Mulsow, J. Grant, S. Roy, A. Grehan, P. Scaps, N. Silverberg, B. Klein, J.-E. Tremblay, and J.-C. Therriault. 2000. Trophic structure of macrobenthos in the Gulf of St. Lawrence and on the Scotian Shelf. *Deep-Sea Research II* **47**: 663-697.
- DFO. 2001. Capelin of the Estuary and Gulf of St. Lawrence. DFO Science, Stock Status Report B4-03.

- DFO. 2002. Shrimp of the Estuary and Gulf of St. Lawrence. DFO Science, Stock Status Report C4-06.
- DFO. 2003a. Chasse au phoque de l'Atlantique, plan de gestion 2000-2005, 35 pp.
[On line: 2003] http://www.dfo-mpo.gc.ca/seal-phoque/reports-rapports/mgtplan-plangest2003/mgtplan-plangest2003_f.htm. (Web pages accessed 06 August 2004).
- DFO. 2003b. Atlantic mackerel of the Northwest Atlantic in 2002. DFO Science, Stock Status Report 2003/010.
- DFO. 2006a. Assessment of the Greenland halibut stock in the Gulf of St. Lawrence (4RST) in 2005. DFO Canadian Science Advisory Secretariat, Science Advisory Report 2006/011.
- DFO. 2006b. Assessment of the Estuary and Gulf of St. Lawrence (Divisions 4RST) capelin stock in 2005. DFO Canadian Science Advisory Secretariat, Science Advisory Report 2006/022.
- DFO. 2007. Accounting for changes in natural mortality in Gulf of St. Lawrence cod stocks. DFO Canadian Science Advisory Secretariat, Science Advisory Report 2007/002.
- Dolgov, A. V. 1997. Distribution, abundance, biomass and feeding of thorny skate, *Raja radiata*, in the Barents Sea. ICES Council Meeting Papers 1997/G:04, 21 pp.
- Dolgov, A. V., and K. V. Revetnyak. 1990. Estimation of rations and food consumption of deep-water redfish (*Sebastes mentella*) from the Norwegian-Barents Sea stock. ICES Council Meeting Papers 1990/G:11, 15 pp.
- Doubleday, W. G. 1981. Manual on groundfish surveys in the NAFO area (revised). NAFO Scientific Council Studies 81/VI/7, 78 pp.
- Durbin, E. G., A. G. Durbin, R. W. Langton, and R. E. Bowman. 1983. Stomach contents of silver hake, *Merluccius bilinearis*, and Atlantic cod, *Gadus morhua*, and estimation of their daily ration. Fishery Bulletin **81**: 437-450.
- Edwards, R. L., and R. E. Bowman. 1979. Food consumed by continental shelf fishes. In Predator-prey systems in fisheries management. Edited by H. Clepper. Washington, D.C., Sport Fishing Institute, pp. 387-406.
- Elliott, J. M., and L. Persson. 1978. The estimation of daily rates of food consumption for fish. Journal of Animal Ecology **47**: 977-991.
- Falkenhaus, T. 1991. Prey composition and feeding rate of *Sagitta elegans* var. *arctica* (chaetognatha) in the Barents Sea in early summer. In Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, 12-16 May 1990. Edited by E. Sakshaug, C. C. E. Hopkins, and N. A. Øritsland. Polar Research **10**, pp. 487-506.
- Fauchald, K., and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. Oceanography and Marine Biological Annual Review **17**: 19-38.
- Feigenbaum, D. 1979. Daily ration and specific daily ration of the chaetognath *Sagitta enflata*. Marine Biology **54**: 75-82.
- Fetter, M., and A. Davidjuka. 1996. Herring daily feeding activity in the Eastern Baltic. ICES Council Meeting Papers 1996/J 26, 10 pp.
- Fontaine, P. M., M. O. Hammill, C. Barrette, and M. C. Kingsley. 1994. Summer diet of the harbour porpoise (*Phocoena phocoena*) in the estuary and the northern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences **51**: 172-178.

- Fréchet, A., J. Gauthier, P. Schwab, L. Pageau, C. Savenkoff, M. Castonguay, D. Chabot, C. Tournois, J.-F. Lussier, J. Spingle, and F. Collier. 2005. L'état du stock de morue du nord du golfe du Saint-Laurent (3Pn, 4RS) en 2004 / The status of cod in the northern Gulf of St. Lawrence (3Pn, 4RS) in 2004. MPO Secrétariat canadien de consultation scientifique Document de Recherche – DFO Canadian Science Advisory Secretariat Research Document, 2005/060.
- Fréchet, A., C. Savenkoff, and J. Gautier. 2006. Mise à jour concernant les mortalités par pêche non comptabilisées / Updates concerning unaccounted fishing mortalities. MPO Secrétariat canadien de consultation scientifique Document de Recherche – DFO Canadian Science Advisory Secretariat Research Document, 2006/086: iv+17 pp.
- Fréchette, J., and S.S.M. Labonté. 1981. Biomass estimate, year-class abundance and mortality rates of *Pandalus borealis* in the northwest Gulf of St. Lawrence. In Proceedings of the International Pandalid Shrimp Symposium. Edited by T. Frady. Kodiak, Alaska, Sea Grant Report 81-3, pp. 307-330.
- Froese, R., and D. Pauly (Editors). 2002. FishBase. World Wide Web electronic publication. [On line: September 2002] <http://www.fishbase.org/search.php>. (Web pages accessed April 2007).
- Gascon, D. (Editor) 2003. Redfish multidisciplinary research zonal program (1995-1998): final report. Canadian Technical Report of Fisheries and Aquatic Sciences No. 2462.
- Gilbert, D., A. F. Vézina, B. Pettigrew, D. P. Swain, P. S. Galbraith, L. Devine, and N. Roy. 1995. État du golfe du Saint-Laurent: conditions océanographiques en 1995. Rapport technique canadien sur l'hydrographie et les sciences océaniques No. 191.
- Grégoire, F., and L. Lefebvre. 2002. Analytical assessment and risk analyses for the stock of spring-spawning herring (*Clupea harengus harengus* L.) on the west coast of Newfoundland (NAFO Division 4R) in 2001. DFO Canadian Science Advisory Secretariat Research Document 2002/059.
- Grégoire, F., L. Lefebvre, and J. Lavers. 2004. Analytical assessment and risk analyses for the spring spawning herring (*Clupea harengus harengus* L.) stock of the west coast of Newfoundland (NAFO Division 4R) in 2003. DFO Canadian Science Advisory Secretariat Research Document 2004/090.
- Grundwald, E., and F. Koster. 1994. Feeding habits of Atlantic cod in west Greenland waters. ICES Council Meeting Papers 1994/P:5, 10 pp.
- Hammill, M. O., and G. B. Stenson. 2000. Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*), and harbour seals (*Phoca vitulina*) in Atlantic Canada. Journal of Northwest Atlantic Fishery Science 26: 1-23.
- Hammill, M. O., C. Lydersen, K. M. Kovacs, and B. Sjare. 1997. Estimated fish consumption by hooded seals (*Cystophora cristata*) in the Gulf of St. Lawrence. Journal of Northwest Atlantic Fishery Science 22: 249-257.
- Hammill, M. O., G. B. Stenson, R. A. Myers, and W. T. Stobo. 1998. Pup production and population trends of the grey seal (*Halichoerus grypus*) in the Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences 55: 423-430.
- Hammill, M. O., G. B. Stenson, F. Proust, P. Carter, and D. McKinnon. 2007. Feeding by grey seals in the Gulf of St. Lawrence and around Newfoundland. NAMMCO Scientific Publications 6: 135-152.

- Harley, S. J., and R. A. Myers. 2001. Hierarchical Bayesian models of length-specific catchability of research trawl surveys. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 1569-1584.
- Haro-Garay, M. J. 2003. Diet and functional morphology of the mandible of two planktonic amphipods from the Strait of Georgia, British Columbia, *Parathemisto pacifica* (Stebbing, 1888) and *Cyphocaris challengerii* (Stebbing, 1888). *Crustaceana, International Journal of Crustacean Research* **76**: 1291-1312.
- Hay, K. A. 1985. Status of the humpback whale, *Megaptera novaeangliae*, in Canada. *Canadian Field-Naturalist* **99**: 425-432.
- Haycock, K. A., and W. Threlfall. 1975. The breeding biology of the herring gull in Newfoundland. *Auk* **92**: 678-697.
- Heise, K. 1997. Life history and population parameters of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*). *Annual Report International Whaling Commission* **47**: 817-825.
- Heymans, J. J., and T. J. Pitcher. 2002. A model of the marine ecosystem of Newfoundland and southern Labrador (2J3KLNO) in the time periods 1985-1987 and 1995-1997. *In* *Ecosystem models of Newfoundland for the time periods 1995, 1985, 1900 and 1450. Edited by T. J. Pitcher, J. J. Heymans, and M. Vasconcelles. Fisheries Centre Research Reports* **10(5)**, pp. 5-43.
- Hop, H., W. M. Tonn, and H. E. Welch. 1997. Bioenergetics of Arctic cod (*Boreogadus saida*) at low temperatures. *Canadian Journal of Fisheries and Aquatic Sciences* **54**: 1772-1784.
- Horwood, J. 1990. *Biology and exploitation of the minke whale*. CRC Press, Boca Raton, FL (USA), 238 pp.
- Hurlbut, T., and G. Poirier. 2001. The status of white hake (*Urophycis tenuis*, Mitchell) in the Southern Gulf of St. Lawrence (NAFO Division 4T) in 2000. *DFO Canadian Science Advisory Secretariat Research Document* 2001/024.
- Hutcheson, M., P. Stewart, and J. Spry. 1981. The biology of benthic communities on the Grand Banks of Newfoundland (including the Hibernia area). *In* *Grand Banks Oceanographic Studies 3. Edited by MacLaren Plansearch, prepared for Mobil Oil*, 99 pp.
- Hutchings, J. A. 2002. Ecology and biodiversity of commercially unexploited marine fishes in the Northwest Atlantic. *Final Report, Dalhousie University, Halifax, Nova Scotia*, 14 pp.
- Ikeda, T., and N. Shiga. 1999. Production, metabolism, and production/biomass (P/B) ratio of *Themisto japonica* (Crustacea: Amphipoda) in Toyama Bay, southern Japan Sea. *Journal of Plankton Research* **21**: 299-308.
- Jackson, G. A., and P. M. Eldridge. 1992. Food web analysis of a planktonic system off southern California. *Progress in Oceanography* **30**: 223-251.
- Jangaard, P. M. 1974. The Capelin (*Mallotus villosus*). Biology, distribution, exploitation, utilization and composition. *Bulletin of the Fisheries Research Board of Canada* **186**, 70 pp.
- Jarre-Teichmann, A., and S. Gu  nette. 1996. Invertebrate benthos. Southern BC Shelf Model. *In* *Mass-balance models of Northeastern Pacific Ecosystems: Proceedings of a workshop held at the Fisheries Centre, University of British Columbia, Vancouver, BC, Canada, November 6-10, 1995. Edited by D. Pauly, V. Christensen, and N. Hagen*, pp. 38-39.
- Jones, B. C., and G. H. Geen. 1977. Food and feeding of spiny dogfish (*Squalus acanthias*) in British Columbia waters. *Journal of the Fisheries Research Board of Canada* **34**: 2067-2078.

- Katona, S. K., S. A. Testaverde, and B. Barr. 1978. Observations on a white-sided dolphin, *Lagenorhynchus acutus*, probably killed in gill nets in the Gulf of Maine. *Fishery Bulletin* **76**: 475-476.
- Kenney, R. D., G. P. Scott, T. J. Thompson, and H. E. Winn. 1997. Estimates of prey consumption and trophic impacts of cetaceans in the USA northeast continental shelf ecosystem. *Journal of Northwest Atlantic Fishery Science* **22**: 155-171.
- Kingsley, M. C. S., and R. R. Reeves. 1998. Aerial surveys of cetaceans in the Gulf of St. Lawrence in 1995 and 1996. *Canadian Journal of Zoology* **76**: 1529-1550.
- Klein, G., E. Rachor, and S. A. Gerlach. 1975. Dynamics and productivity of two populations of the benthic tube-dwelling amphipod *Ampelisca brevicornis* (Costa) in Helgoland Bight. *Ophelia* **14**: 1-2.
- Kotori, M., 1976. The biology of chaetognatha in the Bering Sea and the northern North Pacific Ocean, with emphasis on *Sagitta elegans*. *Memoirs of the Faculty of Fisheries Hokkaido University*. No. 23.
- Lack, D. 1967. Interrelationships in breeding adaptations as shown by marine birds. *Proceedings of the XIV International Ornithology Congress*, pp. 3-42.
- Laurinolli, M. H., L. E. Harris, A. Bundy, and L. P. Fanning. 2004. Compilation of fish stomach data from the Scotian Shelf and Bay of Fundy (1958-2002): CDEENA diet composition and consumption estimation project. *Canadian Technical Report of Fisheries and Aquatic Sciences* No. 2518.
- Lawson, J. W., G. B. Stenson, and D. G. McKinnon. 1993. Diet of harp seals (*Phoca groenlandica*) in 2J3KL during 1991-1993. *NAFO Scientific Council Research Document* 93/36, 15 pp.
- Leblanc, M.-J. 2003. Variations saisonnières en taille et en condition du phoque à capuchon (*Cystophora cristata*) dans le nord-ouest de l'Atlantique. M.Sc. Thesis. Université du Québec à Rimouski.
- Leguerrier, D., N. Niquil, N. Boileau, J. Rzeznik, P.-G. Sauriau, O. Le Moine, and C. Bacher. 2003. Numerical analysis of the food web of an intertidal mudflat ecosystem on the Atlantic coast of France. *Marine Ecology Progress Series* **246**: 17-37.
- Lesage, V., M. O. Hammill, and K. M. Kovacs. 1995. Harbour seal (*Phoca vitulina*) and grey seal (*Halichoerus grypus*) abundance in the St. Lawrence Estuary. *Canadian Manuscript Report of Fisheries and Aquatic Sciences* No. 2307.
- Lesage, V., J. Keays, S. Turgeon, and S. Hurtubise. 2003. Incidental mortality of harbour porpoises in the gillnet fishery of the Estuary and Gulf of St Lawrence in 2000-2002. *DFO Canadian Stock Assessment Secretariat Research Document* 2003/069.
- Lien, J. 1985. Wet and fat: Whales and seals of Newfoundland and Labrador. *Breakwater Books*, St. John's, Newfoundland, 136 pp.
- Lilly, G. R. 1991. Interannual variability in predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) and other prey off southern Labrador and northeastern Newfoundland. *ICES Marine Science Symposia* **193**: 133-146.
- Lilly, G. R., H. Hop, D. E. Stansbury, and C. A. Bishop. 1994. Distribution and abundance of polar cod (*Boreogadus saida*) off southern Labrador and eastern Newfoundland. *ICES Council Meeting Papers* 1994/O 6, 21 pp.
- Lindley, J. A. 1980. Population dynamics and production of euphausiids. 2. *Thysanoessa inermis* and *T. raschi* in the North Sea and American coastal waters. *Marine Biology* **59**: 225-233.

- Lindley, J. A. 1982. Population dynamics and production of euphausiids. 3. *Meganctiphanes norvegica* and *Nyctiphanes couchi* in the North Atlantic Ocean and the North Sea. *Marine Biology* **66**: 37-46.
- Lovrich, G. A., and B. Sainte-Marie. 1997 Cannibalism in the snow crab, *Chionoecetes opilio* (O. Fabricus) (Brachyura: Majidae), and its potential importance to recruitment. *Journal of Experimental Marine Biology and Ecology* **211**: 225-245.
- MacDonald, J. S., and K. G. Waiwood. 1987. Feeding chronology and daily ration calculations for winter flounder (*Pseudopleuronectes americanus*), American plaice (*Hippoglossoides platessoides*), and ocean pout (*Macrozoarces americanus*) in Passamaquoddy Bay, New Brunswick. *Canadian Journal of Zoology* **65**: 499-503.
- Mansfield, A. W., and B. Beck. 1977. The grey seal in eastern Canada. Fisheries and Marine Service Technical Report 704, 81 pp.
- Marsh, H., and D. F. Sinclair. 1989. Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. *Journal of Wildlife Management* **53**: 1017-1024.
- Martin, A. R. 1990. Whales and dolphins. Salamander Press, London and New York, 192 pp.
- Martini, F., M. Lesser, and J. B. Heiser. 1996. Ecology of the hagfish, *Myxine glutinosa* L., in the Gulf of Maine: II. Potential impact on benthic communities and commercial fisheries. *Journal of Experimental Marine Biology and Ecology* **214**: 97-106.
- Mauchline, J. 1980. The biology of Euphausiids. *Advances in Marine Biology* **18**: 373-623.
- Mauchline, J. 1985. Growth and production of Euphausiacea (Crustacea) in the Rockall Trough. *Marine Biology* **90**: 19-26.
- Maunder, J. E., and W. Threlfall. 1972. The breeding biology of the black-legged kittiwake in Newfoundland. *Auk* **89**: 789-816.
- Maurer, R. O., and R. E. Bowman. 1985. Food consumption of squids (*Illex illecebrosus* and *Loligo peali*) off the northeastern United States. In *Biology and ecology of squids Illex illecebrosus and Loligo peali in the northwest Atlantic*. NAFO Scientific Council Studies **9**: 117-124.
- McEachran, J. D., D. F. Boesch, and J. A. Musick. 1976. Food division within two sympatric species-pairs of skates (Pisces: Rajidae). *Marine Biology* **35**: 301-317.
- McKone, W. D., and E. LeGrow. 1983. Thorny and smooth skates. DFO underwater world series UW/21, 5 pp.
- McQuinn, I. H., M. O. Hammill, and L. Lefebvre. 1999. An assessment and risk projections of the west coast of Newfoundland (NAFO division 4R) herring stocks (1965 to 2000). DFO Canadian Stock Assessment Secretariat Research Document 99/119.
- Mehl, S., and T. Westgard. 1983. The diet and consumption of mackerel in the North Sea (a preliminary report). ICES Council Meeting Papers 1983/H 34, 30 pp.
- Mendy, A. N., and E. A. Buchary. 2001. Constructing the Icelandic marine ecosystem model for 1997 using a mass balance modeling approach. In *Fisheries impacts on North Atlantic ecosystems: models and analyses*. Edited by S. Gu  nette, V. Christensen, and D. Pauly. Fisheries Centre Research Reports 9(4), pp. 182-197.
- Metzl, N., B. Moore III, A. Papaud, and A. Poisson. 1989. Transport and carbon exchanges in Red Sea inverse methodology. *Global Biogeochemical Cycles* **3**: 1-26.

- Metzl, N., B. Moore, and A. Poisson. 1990. Resolving the intermediate and deep advective flows in the Indian Ocean by using temperature, salinity, oxygen and phosphate data: the interplay of biogeochemical and geophysical tracers. *Palaeogeography, Palaeoclimatology, Palaeoecology* **89**: 81-111.
- Mills, E. I., and R. O. Fournier. 1979. Fish production and the marine ecosystems of the Scotian Shelf, Eastern Canada. *Marine Biology* **54**: 101-108.
- Mitchell, E. 1973. Draft report on humpback whales taken under specific scientific permit by eastern Canadian land stations, 1969-1971. Report of the International Whaling Commission **23**: 138-154.
- Mitchell, E. 1975. Trophic relationships and competition for food in the northwest Atlantic whales. *Proceedings of the Canadian Zoological Society* 1974: 123-133.
- Montevecchi, W. A., and L. M. Tuck. 1987. Newfoundland birds: Exploitation, study, conservation. Cambridge, Massachusetts, USA, Nuttall Ornithological Club, 272 pp.
- Moore, J. A., G. H. Winters, and L. S. Parsons. 1975. Migrations and biological characteristics of Atlantic mackerel (*Scomber scombrus*) occurring in Newfoundland waters. *Journal of the Fisheries Research Board of Canada* **32**: 1347-1357.
- Morin, R., G. A. Chouinard, I. Forest-Gallant, and G. Poirier. 1998. Assessment of 4T American plaice in 1996 and 1997. DFO Canadian Stock Assessment Secretariat Research Document 98/06.
- Morin, R., I. Forest, and G. Poirier. 2001. Status of NAFO Division 4T American plaice, February 2001. DFO Canadian Science Advisory Secretariat Research Document 2001/023.
- Morissette, L., S.-P. Despatie, C. Savenkoff, M. O. Hammill, H. Bourdages, and D. Chabot. 2003. Data gathering and input parameters to construct ecosystem models for the northern Gulf of St. Lawrence (mid-1980s). Canadian Technical Report of Fisheries and Aquatic Sciences No. 2497.
- NAFO (Editors). 1999. NAFO annual fisheries statistics databases. World Wide Web electronic publication. [On line: 1999] <http://www.nafo.int/fisheries/frames/fishery.html>. (Web pages accessed April 2007).
- Nesis, K. I. 1965. Bioeconoses and biomass of benthos of the Newfoundland-Labrador region. *Fisheries Research Board of Canada Translation Series* **1357**, 75 pp.
- Nichols, F. H. 1975. Dynamics and energetics of three deposit-feeding benthic invertebrate populations in Puget Sound, Washington. *Ecological Monographs* **45**: 57-82.
- Niquil, N., G. A. Jackson, L. Legendre, and B. Delesalle. 1998. Inverse model analysis of the planktonic food web of Takapoto Atoll (French Polynesia). *Marine Ecology Progress Series* **165**: 17-29.
- Ohman, M. D., and J. A. Runge. 1994. Sustained fecundity when phytoplankton resources are in short supply: Omnivory by *Calanus finmarchicus* in the Gulf of St. Lawrence. *Limnology and Oceanography* **39**: 21-36.
- Ohsumi, S. 1979. Interspecies relationships among some biological parameters in cetaceans and estimation of the natural mortality coefficient of the Southern Hemisphere minke whale. Report of the International Whaling Commission **29**: 397-406.
- Okey, T. A., and B. A. Wright. 2004. Toward ecosystem-based extraction policies for Prince William Sound, Alaska: Integrating conflicting objectives and rebuilding pinnipeds. *Bulletin of Marine Science* **74**: 727-747.

- Øresland, V. 2000. Diel feeding of the chaetognath *Sagitta enflata* in the Zanzibar Channel, western Indian Ocean. *Marine Ecology Progress Series* **193**:117-123.
- Pakhomov, E. A., and R. Perissinotto. 1996. Trophodynamics of the hyperiid amphipod *Themisto gaudichaudi* in the South Georgia region during late austral summer. *Marine Ecology Progress Series* **134**: 91-100.
- Panasenko, L.D. 1981. Diurnal rhythms and rations of capelin feeding in the Barents Sea. ICES Council Meeting Papers 1981/H 26.
- Pauly, D. 1989. Food consumption by tropical and temperate fish populations: some generalisations. *Journal of Fish Biology* **35** (Supplement A): 11-20.
- Pauly, D., and V. Christensen (eds.). 1996. Mass-balance models of northeastern Pacific ecosystems. *Fisheries Centre Research Reports* 4: 132 pp.
- Pauly, D., M. L. Soriano-Bartz, and M. L. D. Palomares. 1993. Improved construction, parametrization and interpretation of steady-state ecosystem models. *In* trophic models of aquatic ecosystems. *Edited by* V. Christensen and D. Pauly. Manila (Philippines), ICLARM Conference Proceedings 26, pp. 1-13.
- Pearre, S. Jr. 1981. Feeding by Chaetognatha: energy balance and importance of various components of the diet of *Sagitta elegans*. *Marine Ecology Progress Series* **5**: 45-54.
- Pedersen, S. A., and F. Riget. 1992a. Feeding habits of Greenland halibut, *Reinhardtius hippoglossoides*, in West Greenland waters with special emphasis on predation on shrimp and juvenile redfish. ICES Council Meeting Papers 1992/G:25, 22 pp.
- Pedersen, S. A., and F. Riget. 1992b. Feeding habits of redfish, *Sebastes* sp., in West Greenland waters with special emphasis on predation on shrimp. ICES Council Meeting Papers 1992/G 24, 15 pp.
- Peer, D. L. 1970. Relation between biomass, productivity, and loss to predators in a population of a marine benthic polychaete, *Pectinaria hyperborea*. *Journal of the Fisheries Research Board of Canada* **27**: 2143-2153.
- Pierroti, R. 1983. Gull-puffin interactions on Great Island, Newfoundland. *Biological Conservation* **26**: 1-14.
- Pitcher, T. J., J. J. S. Heymans, and M. Vasconcellos. 2002. Ecosystems models of Newfoundland for the time periods 1995, 1985, 1900 and 1450. *Fisheries Centre Research Reports* 10(5): 74 pp.
- Pitt, T. K. 1982. Recalculation of natural mortality of American plaice from the Grand Bank. NAFO Scientific Council Research Document 82/VI/48, 6 pp.
- Ricker, W. E. 1980. Calcul et interprétation des statistiques biologiques des populations de poissons. *Bulletin of the Fisheries Research Board of Canada* No. 191F.
- Ridgway, S. A., and R. Harrison. 1999. Handbook of marine mammals. Volume 6, The second book of dolphins and the porpoises. Academic Press, Toronto, Ontario, Canada, 486 pp.
- Rivkin, R. B., L. Legendre, D. Deibel, J.-E. Tremblay, B. Klein, K. Crocker, S. Roy, N. Silverberg, C. Lovejoy, F. Mesplé, N. Romero, M. R. Anderson, P. Matthews, C. Savenkoff, and R. G. Ingram. 1996. Vertical flux of biogenic carbon in the ocean: Is there food web control? *Science* **272**: 1163-1166.
- Robertson, A. I. 1979. The relationship between annual production, biomass ratios and life spans for marine macrobenthos. *Oecologia* **38**: 193-202.

- Rodriguez-Marin, E., A. Punzon, J. Paz, and I. Olaso. 1994. Feeding of the most abundant fish species in Flemish Cap in summer 1993. NAFO Scientific Council Research Document 94/35, 33 pp.
- Ross, S. 1993. Food and feeding of the hooded seal in Newfoundland. M.Sc. thesis. Memorial University of Newfoundland, St. John's, Newfoundland.
- Roy, S., N. Silverberg, N. Romero, D. Deibel, B. Klein, C. Savenkoff, A. F. Vézina, J.-E. Tremblay, L. Legendre, and R. B. Rivkin. 2000. Importance of mesozooplankton feeding for the downward flux of biogenic carbon in the Gulf of St. Lawrence (Canada). *Deep-Sea Research II* 47: 519-544.
- Rudstam, L. G., S. Hansson, S. Johansson, and U. Larsson. 1992. Dynamics of planktivory in a coastal area of the northern Baltic Sea. *Marine Ecology Progress Series* 80: 159-173.
- Sameoto, D. D. 1976. Respiration rates, energy budgets, and molting frequencies of three species of euphausiids found in the Gulf of St. Lawrence. *Journal of the Fisheries Research Board of Canada* 33: 2568-2576.
- Sameoto, D. D. 1987. Vertical distribution and ecological significance of chaetognaths in the Arctic environment of Baffin Bay. *Polar Biology* 7: 317-328.
- Sanders, H. L. 1956. The biology of marine bottom communities. Oceanography of Long Island Sound. X. *In* Oceanography of Long Island Sound, 1952-1954. Edited by G. A. Riley, S. A. M. Conover, G. B. Deevey, R. J. Conover, S. B. Wheatland, E. Harris, and H. L. Sanders. Bulletin of the Bingham Oceanography Collection. New Haven, Conn., 15, pp. 345-414.
- Santos, M. B., G. J. Pierce, H. M. Ross, R. J. Reid, and B. Wilson. 1994. Diets of small cetaceans from the Scottish coast. ICES Council Meeting Papers 1994/N:11, 16 pp.
- Savard, L., and Bouchard, B. 2004. État des stocks de crevette (*Pandalus borealis*) de l'estuaire et du golfe du Saint-Laurent en 2003. Secrétariat canadien de consultation scientifique du MPO, Document de recherche 2004/091.
- Savenkoff, C., A. F. Vézina, T. T. Packard, N. Silverberg, J.-C. Therriault, W. Chen, C. Bérubé, A. Mucci, B. Klein, F. Mesplé, J.-E. Tremblay, L. Legendre, J. Wesson, and R. G. Ingram. 1996. Distributions of oxygen, carbon, and respiratory activity in the deep layer of the Gulf of St. Lawrence and their implications for the carbon cycle. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 2451-2465.
- Savenkoff, C., A. F. Vézina, S. Roy, B. Klein, C. Lovejoy, J.-C. Therriault, L. Legendre, R. Rivkin, C. Bérubé, J.-E. Tremblay, and N. Silverberg. 2000. Export of biogenic carbon and structure and dynamics of the pelagic food web in the Gulf of St. Lawrence Part 1. Seasonal variations. *Deep-Sea Research II* 47: 585-607.
- Savenkoff, C., A. F. Vézina, and A. Bundy. 2001. Inverse analysis of the structure and dynamics of the whole Newfoundland-Labrador Shelf ecosystem. Canadian Technical Report of Fisheries and Aquatic Sciences No. 2354.
- Savenkoff, C., H. Bourdages, M. Castonguay, L. Morissette, D. Chabot, and M. O. Hammill. 2004b. Input data and parameter estimates for ecosystem models of the northern Gulf of St. Lawrence (mid-1990s). Canadian Technical Report of Fisheries and Aquatic Sciences No. 2531.
- Savenkoff, C., H. Bourdages, D. P. Swain, S.-P. Despatie, J. M. Hanson, R. Méthot, L. Morissette, and M. O. Hammill. 2004c. Input data and parameter estimates for ecosystem models of the southern Gulf of St. Lawrence (mid-1980s and mid-1990s). Canadian Technical Report of Fisheries and Aquatic Sciences No. 2529.

- Savenkoff, C., M. Castonguay, A. F. Vézina, S.-P. Despatie, D. Chabot, L. Morissette, and M. O. Hammill. 2004a. Inverse modelling of trophic flows through an entire ecosystem: the northern Gulf of St. Lawrence in the mid-1980s. *Canadian Journal of Fisheries and Aquatic Sciences* **61**: 2194-2214.
- Savenkoff, C., M. Castonguay, R. Méthot, D. Chabot, and M. O. Hammill. 2005. Input data and parameter estimates for ecosystem models of the northern Gulf of St. Lawrence (2000–2002). *Canadian Technical Report of Fisheries and Aquatic Sciences* No. 2588.
- Savenkoff, C., M. Castonguay, D. Chabot, M. O. Hammill, H. Bourdages, and L. Morissette. 2007. Changes in the northern Gulf of St. Lawrence ecosystem estimated by inverse modelling: Evidence of a fishery-induced regime shift? *Estuarine, Coastal and Shelf Science* **73**: 711-724.
- Schwalme, K., and G. A. Chouinard. 1999. Seasonal dynamics in feeding, organ weights, and reproductive maturation in Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. *ICES Journal of Marine Science* **56**: 303-319.
- Scott, W. B., and M. G. Scott. 1988. Atlantic fishes of Canada. *Canadian Bulletin of Fisheries and Aquatic Sciences* **219**, 731 pp.
- Sergeant, D. E. 1991. Harp seals, man and ice. *Canadian Special Publication of Fisheries and Aquatic Sciences* **114**, 163 pp.
- Sergeant, D. E., D. J. St. Aubin, and J. R. Geraci. 1980. Life history and northwest Atlantic status of the Atlantic white-sided dolphin, *Lagenorhynchus acutus*. *Cetology* **37**: 1-12.
- Shader, M. 1977. Production and population dynamics of *Ampelisca tenuicornis* (Amphipoda) with notes on the biology of its parasite *Sphaeronella longipes* (Copepoda). *Journal of the Marine Biological Association of the United Kingdom* **57**: 955-968.
- Shader, M., and F. Evans. 1975. Feeding and gut structure of *Parathemisto gaudichaudi* (Guerin) (Amphipoda, Hyperiidea). *Journal of the Marine Biological Association of the United Kingdom* **55**: 641-656.
- Silverberg, N., B. Sundby, A. Mucci, S. Zhong, T. Arakaki, P. Hall, A. Landen, and A. Tengberg. 2000. Remineralization of organic carbon in eastern Canadian continental margin sediments. *Deep-Sea Research II* **47**: 699-731.
- Simon, J. E., and K. T. Frank. 1995. An assessment of the skate fishery in Division 4VsW. DFO Atlantic Fisheries Research Document 1995/71.
- Sinclair, A. F. 2001. Natural mortality of cod (*Gadus morhua*) in the Southern Gulf of St. Lawrence. *ICES Journal of Marine Science* **58**: 1-10.
- Sjare, B., G. B. Stenson, and E. A. Perry. 1996. Summary of the catch and catch-at-age data for harp seals in the northwest Atlantic, 1946-94. *NAFO Scientific Council Studies* **26**: 33-39.
- Steimle, F. W. J. 1985. Biomass and estimated productivity of the benthic macrofauna in the New York Bight: A stressed coastal area. *Estuarine, Coastal and Shelf Science* **21**: 539-554.
- Steimle, F. W. J. 1987. Benthic faunal production. *In* Georges Bank. *Edited by* R. H. Backus, MIT Press, Cambridge, Mass., pp. 310-314.
- Stoecker, D. K., and J. M. Capuzzo. 1990. Predation on Protozoa: its importance to zooplankton. *Journal of Plankton Research* **12**: 891-908.
- Strong, K. W. 1981. Seasonal occurrence and distribution of zooplankton in waters over the Grand Banks of Newfoundland. *In* Grand Banks Oceanographic Studies. *Edited by* MacLaren Plansearch, prepared for Mobil Oil, 32 pp.

- Sullivan, B. K. 1980. *In situ* feeding behavior of *Sagitta elegans* and *Eukrohnia hamata* (Chaetognatha) in relation to the vertical distribution and abundance of prey at Ocean Station 'P'. *Limnology and Oceanography* **25**: 317-326.
- Tanaka, S. 1990. Estimation of natural mortality coefficient of whales from the estimates of abundance and age composition data obtained from research catches (SC/41/O 15). Report of the International Whaling Commission **40**: 531-536.
- Tanasichuk, R. W., D. M. Ware, W. Shaw, and G. A. McFarlane. 1991. Variations in the diet, daily ration, and feeding periodicity of Pacific hake (*Merluccius productus*) and spiny dogfish (*Squalus acanthus*) off the lower west coast of Vancouver Island. *Canadian Journal of Fisheries and Aquatic Sciences* **48**: 2118-2128.
- Thompson, R. J., and M. Hawryluk. 1990. Physiological energetics of the snow crab, *Chionoecetes opilio*. In *Proceedings of the International Symposium on King & Tanner Crabs*. Edited by A. S. G. C. Program. November 1989, Anchorage, Fairbanks, Alaska, USA, Lowell Wakefield, pp. 283-293.
- Threlfall, W. 1968. The food of three species of gulls in Newfoundland. *Canadian Field-Naturalist* **82**: 176-180.
- Toda, H., T. Arima, M. Takahashi, and S.-E. Ichimura. 1987. Physiological evaluation of temperature effect on the growth processes of the mysid, *Neomysis intermedia* Czerniawsky. *Journal of Plankton Research* **9**: 51-63.
- Tonnesson, K., and P. Tiselius. 2005. Diet of the chaetognaths *Sagitta setosa* and *S. elegans* in relation to prey abundance and vertical distribution. *Marine Ecology Progress Series* **289**: 177-190.
- Trites, A. W., V. Christensen, and D. Pauly. 1997. Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. *Journal of Northwest Atlantic Fishery Science* **22**: 173-187.
- Varpe, Ø., Ø. Fiksen, and A. Slotte. 2005. Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. *Oecologia* **146**: 443-451.
- Vesin, J. P., W. C. Leggett, and K. W. Able. 1981. Feeding ecology of capelin (*Mallotus villosus*) in the estuary and western Gulf of St. Lawrence and its multispecies implications. *Canadian Journal of Fisheries and Aquatic Sciences* **38**: 257-267.
- Vézina, A. F., and M. L. Pace. 1994. An inverse model analysis of planktonic food webs in experimental lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **51**: 2034-2044.
- Vézina, A. F., and M. Pahlow. 2003. Reconstruction of ecosystem flows using inverse methods: how well do they work? *Journal of Marine Systems* **40-41**: 55-77.
- Vézina, A. F., and T. Platt. 1988. Food web dynamics in the ocean. I. Best-estimates of flow networks using inverse methods. *Marine Ecology Progress Series* **42**: 269-287.
- Vézina, A. F., and C. Savenkoff. 1999. Inverse modeling of carbon and nitrogen flows in the pelagic food web of the Northeast Subarctic Pacific. *Deep-Sea Research II* **46**: 2909-2939.
- Vézina, A. F., F. Berreville, and S. Lozab. 2004. Inverse reconstructions of ecosystem flows in investigating regime shifts: impact of the choice of objective function. *Progress in Oceanography* **60**: 321-341.
- Vézina, A. F., C. Savenkoff, S. Roy, B. Klein, R. Rivkin, J.-C. Therriault, and L. Legendre. 2000. Export of biogenic carbon and structure and dynamics of the pelagic food web in the Gulf of St. Lawrence Part 2. Inverse analysis. *Deep-Sea Research II* **47**: 609-635.

- Vinter, M. 1989. Some notes on the biology of the starry ray, *Raja radiata*, in the North Sea, as reported in Anon 1989. Report of the Multispecies Assessment Working Group. ICES Council Meeting Papers 1989/Assess **20**: 41-43.
- Waiwood, K. G., J. Majkowski, and G. Keith. 1980. Food habits and consumption rates of cod from the southwestern Gulf of St. Lawrence (1979). Canadian Atlantic Fisheries Scientific Advisory Committee Research Document 80/37.
- Waldron, D. E. 1988. Trophic biology of the silver hake (*Merluccius bilinearis*) population on the Scotian Shelf. Ph. D. Thesis, Dalhousie University, Halifax, N. S.
- Waring, G. T., D. L. Palka, P. J. Clapham, S. Swartz, M. C. Rossman, T. V. N. Cole, L. J. Hansen, K. D. Bisack, K. D. Mullin, R. S. Wells, D. K. Odell, and N. B. Barros. 1999. Long-finned pilot whale (*Globicephala melas*): Western North Atlantic stock. U.S. Atlantic and Gulf of Mexico Marine Mammal Stock Assessments – 1999. Woods Hole, Massachusetts, U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Science Center. NMFS-NE-153: 75-85.
- Warwick, R. M., C. L. George, and J. R. Davies. 1978. Annual macrofauna production in a *Venus* community. Estuarine and Coastal Marine Science **7**: 215-241.
- Wetherbee, B. M., and E. Cortés. 2004. Food consumption and feeding habits. In Biology of sharks and their relatives. Edited by J. C. Carrier, J. A. Musick, and M. R. Heithaus. CRC Press, Boca Raton, pp. 225-246.
- Wilson, M. T., C. M. Jump, and J. T. Duffy-Anderson. 2006. Comparative analysis of the feeding ecology of two pelagic forage fishes: capelin *Mallotus villosus* and walleye pollock *Theragra chalcogramma*. Marine Ecology Progress Series **317**: 245-258.
- Winberg, G. G. 1956. Rate of metabolism and food requirements of fish. Fisheries Research Board of Canada Translation Series 194.
- Zamarro, J. 1992. Feeding behaviour of the American plaice (*Hippoglossoides platessoides*) on the southern Grand Banks of Newfoundland. Netherlands Journal of Sea Research **29**: 229-238.

Appendix 1. Flows (in $\text{t km}^{-2} \text{ yr}^{-1}$; 472 flows) estimated by inverse modelling and weighting applied during the estimation. Var: variance, CV: coefficient of variation, B: biomass, Q: consumption, DC: proportion in diet (by mass), Obs: locally observed.

Flows	Description
Respiration (30 flows)	
Weight:	$\text{Var}(B_y^{obs})$
Notation:	R_y
Respiration of group y . No respiration term for phytoplankton.	
Egestion (29 flows)	
Weight:	$\text{Var}(B_y^{obs})$
Notation:	D_y
Flow of group y to detritus (detrital flow or non-assimilated food). No egestion term for phytoplankton (included in mortality term) or detritus.	
Other mortality causes (30 flows)	
Weight:	$\text{Var}(B_y^{obs})$
Notation:	MO_y
Natural mortality other than predation of group y including diseases and other natural causes of death (flow to detritus). No mortality term for detritus.	
Predation (361 flows)	
Weight:	$\text{Var}(Pr_{x \rightarrow y}) = (Q_y^{obs})^2 * (CV(DC_{x \rightarrow y}^{obs})^2 + CV(Q_y^{obs})^2)$
Notation:	$Pr_{x \rightarrow y}$
Predation of group x by group y based on the diet composition of each group.	
Export (21 flows)	
Weight:	$\text{Var}(EX_y^{obs})$
Notation:	EX_y
Export (including catches) of group y out of the system. No export term for several groups (whales, hooded seals, small demersals, small crabs, echinoderms, polychaetes, other benthic invertebrates, large and small zooplankton groups, and phytoplankton).	
Phytoplankton production (1 flow)	
Weight:	$\text{Var}(P_{phy}^{obs})$
Notation:	P_{phy}
Net primary production corrected for respiration.	

Appendix 2. Mass balance and data equations (179 equations) and corresponding weights used in inverse modelling. Var: variance; CV: coefficient of variation; B: biomass; Q: consumption; DC: proportion in diet (by mass); Obs: locally observed; ϵ : residual, the difference between observations and model estimates.

Mass

balance for

Description

Consumers (29 eqs.)

Weight: $\text{Var}(B_y^{obs})$

Equation:
$$\sum_x Pr_{x \rightarrow y} - R_y - D_y - \sum_u Pr_{y \rightarrow u} - MO_y - EX_y = \Delta B_y + \epsilon$$

For a consumer y , consumption ($\sum_x Pr_{x \rightarrow y}$) representing the input must balance the sum of the outputs consisting of respiration (R_y), egestion (detrital flow, D_y), natural mortality (predation by other groups [$\sum_u Pr_{y \rightarrow u}$], and other natural causes of death [MO_y]) and fishing mortality (export, EX_y). We assumed that there was no change in biomass ($\Delta B_y = 0$), except for harp seals ($\Delta B_y = -8.19 \times 10^{-3} \text{ t km}^{-2} \text{ yr}^{-1}$).

Phytoplankton (1 eq.)

Weight: $\text{Var}(B_{phy}^{obs})$

Equation:
$$P_{phy} - MO_{phy} - \sum_y Pr_{phy \rightarrow y} = 0 + \epsilon$$

Net (corrected for respiration) production (P_{phy}) must balance the sum of the outputs (phytoplankton mortality including the egestion term [MO_{phy}] and consumption of phytoplankton by other groups [$\sum_y Pr_{phy \rightarrow y}$]).

Detritus (1 eq.)

Weight: $\text{Var}(B_{Det}^{obs})$

Equation:
$$\sum_x D_x + \sum_x MO_x - \sum_y Pr_{Det \rightarrow y} - R_{Det} - EX_{Det} = 0 + \epsilon$$

Inputs (egestion [$\sum_x D_x$] and other natural causes of death [$\sum_x MO_x$] for other groups) must balance the sum of the outputs (consumption of detritus by other groups [$\sum_y Pr_{Det \rightarrow y}$], bacterial remineralization of detritus [R_{Det}], and burial [EX_{Det}]). As bacteria were considered part of the detritus, detritus was assumed to respire.

Appendix 2. Cont.

Mass balance for	Description
Export (18 eqs.)	
Weight:	$\text{Var}(EX_y^{obs})$
Equation:	$EX_y^{obs} = EX_y + \epsilon$
	Export estimated by inverse modelling (EX_y) is equal to observed export (EX_y^{obs}) from local field studies (except for harp seals, seabirds, and detritus).
Predation ^a (130 eqs.)	
Weight:	$\text{Var}(Pr_{u \rightarrow y}) = (Q_y^{obs})^2 * (CV(DC_{u \rightarrow y}^{obs})^2 + CV(Q_y^{obs})^2)$
Equation:	$DC_{u \rightarrow y}^{obs} = \frac{Pr_{u \rightarrow y}}{\sum_x Pr_{x \rightarrow y}} + \epsilon$
	Proportion of the prey u in the diet (by mass) of consumer y estimated by inverse modelling ($\frac{Pr_{u \rightarrow y}}{\sum_x Pr_{x \rightarrow y}}$) is equal to the observed diet proportion ($DC_{u \rightarrow y}^{obs}$) from local field studies or available only as low estimates with low SD (< 0.6%).

^a Note that the weight of the additional diet equations (predation) for groups with no information on diet proportion variability is the average of all known coefficients of variation for diet proportion ($CV(DC_{u \rightarrow y}^{obs})_{\text{mean}} = 167\%$). Q_y^{obs} is observed consumption from local field studies or the literature ($CV(Q_y^{obs})_{\text{mean}} = 96\%$).

Appendix 3. Constraints (1226 constraints) used in the inverse modelling.

Constraint for	Description
Non-negativity (472 constraints)	
Inequality:	$R_y \geq 0; D_y \geq 0; MO_y \geq 0; Pr_{x \rightarrow y} \geq 0; EX_y \geq 0; P_{phy} \geq 0$
All the unknown flows are non-negative.	
Growth efficiency (58 constraints)	
Inequality:	$GE_y^{\min} < \frac{\sum_x Pr_{x \rightarrow y} - R_y - D_y}{\sum_x Pr_{x \rightarrow y}} < GE_y^{\max}$
Growth efficiency (of food conversion; GE = production/consumption) ranges: 0.1–1% for marine mammals and seabirds; 10–30% for fish, shrimp, crabs, and large zooplankton; 9–30% for benthic invertebrates; and 25–50% for small zooplankton (Christensen and Pauly 1992).	
Assimilation efficiency (58 constraints)	
Inequality:	$AE_y^{\min} < \frac{\sum_x Pr_{x \rightarrow y} - D_y}{\sum_x Pr_{x \rightarrow y}} < AE_y^{\max}$
Assimilation efficiency (AE) ranges between 70 and 90% for all the groups (Winberg 1956) except for large and small zooplankton (50–90%) (Christensen and Pauly 1992).	
Ecotrophic efficiency (60 constraints)	
Inequality:	$EE_y^{\min} < \frac{\sum_x Pr_{x \rightarrow y} - R_y - D_y - MO_y}{\sum_x Pr_{x \rightarrow y} - R_y - D_y} < EE_y^{\max}$
Ecotrophic efficiency (EE: production exported or consumed within the system) ranges between 0 and 0.95 for all groups except for detritus (no constraint ^a) (Christensen and Pauly 1992).	

Appendix 3. Cont.

Constraint for	Description
Consumption (58 constraints)	
Inequality:	$Q_y^{\min} < \sum_x Pr_{x \rightarrow y} < Q_y^{\max}$
	Predation of group x by group y ($\sum_x Pr_{x \rightarrow y}$) ranges between the minimum and maximum observed consumption values.
Export (6 constraints)	
Inequality:	$Exp_y^{\min} < EX_y < Exp_y^{\max}$
	Export of group y ranges between the minimum and maximum observed values (i.e., harp seals, seabirds, and detritus).
Predation (458 constraints)	
Inequality:	$DC_{u \rightarrow y}^{\min} < \frac{Pr_{u \rightarrow y}}{\sum_x Pr_{x \rightarrow y}} < DC_{u \rightarrow y}^{\max}$
	Proportion of the prey u in the diet (by mass) of consumer y ranges between the minimum and maximum observed values.

Appendix 3. Cont.

Constraint for	Description
Production (60 constraints)	
Inequality:	$P_y^{\min} < \sum_x Pr_{x \rightarrow y} - R_y - D_y < P_y^{\max}$
Production of group y ranges between the minimum and maximum observed values.	
Respiration of large and small zooplankton (2 constraints)	
Inequality:	$0.20 * \sum_x Pr_{x \rightarrow y} < R_y$
Respiration (R_y) of zooplankton groups y is at least 20% of total consumption ($\sum_x Pr_{x \rightarrow y}$) (Vézina and Pace 1994).	
Respiration (2 constraints)	
Inequality:	$R_y^{\min} < R_y < R_y^{\max}$
Bacterial respiration ranges between the minimum and maximum observed values.	

^a: The ecotrophic efficiency of the detritus group is defined as the ratio of what flows out of a detritus box to what flows into that same box (Christensen and Pauly 1992). Under the steady state assumption, this ratio should be equal to 1 if the mass balance residual of detritus is "0".

Appendix 4. Estimated values (in $\text{t km}^{-2} \text{yr}^{-1}$) from the final solution based on 31 balanced and ecologically realistic random perturbations. P_i : production; Q_i : consumption; R_i : respiration; D_i : egestion (detrital flow); MO_i : other mortality; EX_i : fishing mortality (export); SD: standard deviation.

Group	P_i	$\pm\text{SD}$	Q_i	$\pm\text{SD}$	R_i	$\pm\text{SD}$	D_i	$\pm\text{SD}$	MO_i	$\pm\text{SD}$	EX_i	$\pm\text{SD}$
Mysticeti	0.02	0.01	1.92	0.54	1.35	0.41	0.56	0.19	0.02	0.01		
Odontoceti	0.004	0.001	0.42	0.06	0.31	0.08	0.11	0.04	0.004	0.001	2.06×10^{-4}	5.14×10^{-5}
Harp seals	0.016	0.001	1.64	0.15	1.18	0.12	0.45	0.11	0.001	0.001	2.35×10^{-2}	4.59×10^{-4}
Hooded seals	0.001	0.000	0.08	0.02	0.06	0.01	0.02	0.00	0.001	0.000		
Grey and harbour seals	0.004	0.000	0.41	0.12	0.29	0.02	0.12	0.02	0.004	0.000	2.93×10^{-5}	1.47×10^{-5}
Seabirds	0.001	0.000	0.13	0.09	0.10	0.10	0.03	0.04	0.001	0.000	1.58×10^{-4}	0
Large cod	0.18	0.03	1.12	0.18	0.64	0.17	0.30	0.11	0.018	0.019	2.80×10^{-2}	7.31×10^{-3}
Small cod	0.05	0.00	0.20	0.04	0.10	0.05	0.04	0.02	0.002	0.000	7.02×10^{-5}	1.96×10^{-5}
Large Green. halibut	0.14	0.00	0.60	0.03	0.34	0.07	0.13	0.06	0.05	0.01	3.65×10^{-2}	1.76×10^{-3}
Small Green. halibut	0.53	0.03	1.76	0.04	0.84	0.18	0.39	0.17	0.43	0.03	6.97×10^{-4}	4.40×10^{-5}
Amer. plaice	0.13	0.04	0.53	0.19	0.30	0.24	0.10	0.09	0.01	0.01	1.43×10^{-3}	1.55×10^{-4}
Flounders	0.03	0.00	0.14	0.05	0.08	0.07	0.03	0.02	0.002	0.001	4.21×10^{-3}	5.01×10^{-4}
Skates	0.02	0.00	0.10	0.04	0.05	0.03	0.03	0.01	0.02	0.00	3.84×10^{-4}	1.16×10^{-4}
Redfish	0.54	0.00	4.94	0.46	3.02	0.41	1.38	0.29	0.16	0.00	5.25×10^{-3}	3.53×10^{-4}
Large demersals	0.06	0.01	0.24	0.09	0.15	0.13	0.04	0.02	0.01	0.01	3.95×10^{-3}	2.88×10^{-4}
Small demersals	0.29	0.01	1.54	0.45	0.91	0.27	0.34	0.18	0.01	0.00		
Capelin	5.14	0.85	35.12	8.52	21.53	7.30	8.44	4.27	0.97	0.73	7.00×10^{-2}	8.19×10^{-3}
Large pelagics	0.01	0.00	0.03	0.01	0.02	0.01	0.01	0.01	0.0003	0.0000	2.53×10^{-5}	9.53×10^{-6}
Pisci. small pel. feeders	0.50	0.01	2.14	0.81	1.18	0.69	0.45	0.27	0.03	0.01	2.10×10^{-1}	2.89×10^{-2}
Plank. small pel. feeders	1.33	0.19	6.31	3.03	3.25	2.82	1.73	1.07	0.07	0.01	1.57×10^{-1}	8.62×10^{-3}

Appendix 4. Cont.

Group	P _i	±SD	Q _i	±SD	R _i	±SD	D _i	±SD	MO _i	±SD	EX _i	±SD
Shrimp	3.93	0.64	17.75	6.39	9.94	6.08	3.87	2.40	0.24	0.23	3.03×10^{-1}	1.84×10^{-2}
Large crabs	0.48	0.04	4.81	0.31	2.95	0.42	1.37	0.25	0.43	0.04	5.07×10^{-2}	1.33×10^{-3}
Small crabs	0.17	0.00	1.24	0.38	0.77	0.45	0.29	0.19	0.01	0.00		
Echinoderms	19.46	1.46	82.28	54.32	45.14	44.41	17.68	13.92	17.51	1.31		
Molluscs	29.74	1.19	118.58	67.60	54.76	46.22	34.08	21.32	26.76	1.07	5.32×10^{-3}	3.31×10^{-4}
Polychaetes	18.92	12.56	82.32	68.85	43.29	63.20	20.11	29.91	6.75	9.77		
Other benthic invertebrates	8.50	1.29	40.07	33.64	22.13	21.45	9.43	11.39	5.85	0.95		
Large zooplankton	48.50	12.40	182.62	47.11	91.73	58.31	42.39	41.44	2.42	0.62		
Small zooplankton	656.88	434.03	1537.79	815.32	440.74	514.92	440.17	392.86	133.66	201.49		
Phytoplankton	1575.07	676.18							378.52	326.10		
Detritus					769.86	342.10					5.72×10^1	0.55×10^1

Appendix 5. Comparisons between the a priori coefficients of variation of the input data and a posteriori coefficients of variation of the estimated flows for the 2003–2005 period.

	Mean	Mean
	a priori	a posteriori
	CVs	CVs
Production	71%	16%
Consumption	96%	34%
Predation	167%	68%
Export	38%	14%
Respiration	51% ^a	57%
Detrital flow	51% ^a	61%
Other mortality	51% ^a	42%

^a Due to a lack of information, we used the average of all observed coefficients of variation for biomass. However, these a priori CVs should be considered as minimum values. The biomass values of the seal groups estimated from the model of Hammill and Stenson (2000) with no information on biomass variability were not used here in the average of all known coefficients of variation for biomass.

Appendix 6. Number of active constraints for different parameters (estimation period. Only the estimates based on the upper and lower constraint limit perturbation; final solution: mean of 31 balanced iterations. P_i : production food not assimilated, GE_i : growth efficiency, EE_i : ecotrophic efficiency, D : R_i : respiration.

		P_i	Q_i	EX_i
Initial solution	Number of active constraints	9	4	2
	Number of total estimates	30	29	3
	% of active constraints	30%	14%	67%
Final solution	Number of active constraints	4	0	1
	Number of total estimates	30	29	3
	% of active constraints	13%	0%	33%

ates at the limit set by the constraints) for the 2003–2005
 nits are used here. Initial solution: first inversion without
 , Q_i : consumption, EX_i : export, $GS_i (=1-AE_i)$: proportion of
 $C_{u \rightarrow y}$: proportion of prey u in diet (by mass) of consumer y ,

Flow/efficiency					
GS_i	GE_i	EE_i	$DC_{u \rightarrow y}$	R_i	Total
10	10	9	39	0	83
29	29	30	229	3	382
34%	34%	30%	17%	0%	22%
1	2	5	9	0	22
29	29	30	229	3	382
3%	7%	17%	4%	0%	6%

